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ACQUIRED SPECIFIC REACTIONS TO COLOR (CHROMOTROPISM) IN *OREGONIA GRACILIS*

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Seven figures

OUTLINE

I. INTRODUCTION

It has long been known that certain genera of the long-legged spider crabs place foreign bodies upon their legs and carapaces. This act is sometimes called a disguising and sometimes an act of decoration according to the interpretation which is put upon

it by the observer. In the citations which follow, disguise is the motive usually assigned to the animals. Thus in The Cambridge Natural History, "Crustacea and Arachnids"[1] Smith writes: "The Spider crabs do not burrow, and their respiratory mechanism is simple; but since they are forms that clamber about among weeds, etc., upon the sea bottom, they often show remarkable protective resemblances to their surroundings, which are not found in the cyclometopa. * * * But besides this, the long-legged forms such as Inachus, Hyas, etc., have the habit of planting out Zoophytes, Sponges and Algae upon their spiny carapaces, so that they literally become part and parcel of the organic surroundings among which they live. It may perhaps be wondered what are the enemies which these armoured crustacea fear." Similarly in the Riverside Natural History[2] the writer, J. S. Kingsley, states "Some of these forms keep their shells perfectly clean, seeming to rely upon their general resemblance to the Sertularians and other hydrozoa, among which they dwell, for protection. Others, however, permit all sorts of foreign bodies, both animal and plants, to become attached to their bodies, so that they are effectually concealed, and even when moving it seems as if a small forest of sea-weed were being transplanted to another locality." In the sentences just quoted the motive attributed to the animal is again concealment, although the foreign bodies are said to be permitted to become attached. Leunis[3] in discussing the same group of animals says of them: "Die meisten haben traege, langsame Bewegungen und tragen auf ihrer Oberfläche oft einen mehr oder weniger dichten Besatz. von Pflanzen und festsitzenden Thieren (Hydroidenpolypen, Schwämen, u. s. w.) durch welchen sie leichterer vor den Nachstelligungen ihrer Feinde verbergen können."

It is evident from the quotations which have just been cited, that the authors entertain different views as to the manner in which the foreign bodies come to be upon the carapaces of the crabs. According to one, the Zoophytes, etc., are "planted out;" according to another, the plant and animal forms are "permitted" to become attached to the body of the crab. It soon

[1] Crustacea and Arachnids, p. 192.
[2] Vol. II, p. 61.
[3] Zoologie, Bd. II, 649.

became apparent to the writer, after a preliminary study of the habit of decoration in *Oregonia gracilis*, that a distinction should be made between what may be called *active* and *passive* decoration. Cursory observation of the crabs is sufficient to reveal the curious habit or instinct of self adornment. The animals do actually "plant out" algae, etc., upon their bodies. On the other hand, the writer doubts whether barnacles, tunicates, sponges, hydrozoa and tubeworms are placed upon the carapace by the active effort of the animal. Certainly, the writer never observed an active decoration of the crabs with such material, during a period of observation extending over seven weeks. Triton eggs were the only objects of a similar nature which were so used. On the other hand, the attachment of forms which simply happened to settle down upon the crab as it rested upon the bottom of the aquarium, was repeatedly observed. In one instance a sea-anemone (Metridium) 35 mm. in length when expanded, attached itself to the shell of a Mytilus which was already attached to the carapace of an *Oregonia gracilis* when captured. Passive decoration [4] must therefore be recognized.

The manner in which the active decoration or "planting out" takes place is worthy of description. Minkiewicz [5] supplementing his own observations by those of Aurivillius, has described the movements very exactly. "Le procédé de déguisement a été tres exactement décrit par Carl Aurivillius chez *Hyas araneus* L. de la famille des Majinae. Comme il est presque identique à celui de Maja, je n'y insisterai pas beaucoup. Ayant trouvé une algue (n'importe laquelle: rouge, brune, ou verte—cela dépend seulement de l'entourage), le crabe l'attrape avec ses pinces grêles et allongées, la met d'abord dans 'sa bouche' et en la tenant par un bout avec ses maxillipedes se met à la déchirer en morceaux avec les deux pinces, l'une l'attirant vers sa carapace, l'autre la repoussant.

[4] Since this paragraph was written, the author has found that C. Aurivillius made the same distinction and employed the same words as are here used, "Unter solchen Umständen stellt sich die *erste* und zwar die wichtigste Frage folgendermassen auf: Verhalt sich die Krabbe aktiv oder passiv hinsichtlich des Kleides fremder Organismen, welches ihren Körper bedeckt" P. 6, Die Maskirung der Oxyrhynchen Dekapoden durch besondere Anpassungen ihres Körperbaues vermittelt. *Svenska Vet. Akad. Handl.*, vol. XXIII. Stockholm.

[5] Analyse Expérimentale de l'instinct de Déguisement chez les Brachyures Oxyrhynques. (Note préliminaire.) *Arch. de Zoologie Expér. et Gén.*, t. 7, p. 36.

"Un morceau, de taille et de forme variable infiniment étant une fois découpé le crabe le pousse avec une de ses pinces entre les maxillipedes et le fait tourner plusieurs fois en procédant comme s'il s'agissait d'une proie, d'une moule ou d'un morceau de poisson par exemple.

"Apres l'avoir froissé, il le prend de nouveau avec une de ses pinces la gauche ou la droite sans distinction, puis étend la pince en avant autant que possible, et ayant fait un mouvement de rotation il recourbe la pince sur son dos, et se met alors à accrocher l'algue sur un groupe de crochets dorsaux, rostraux, branchiaux, etc., en maniant la pince a petits mouvements de va et viens, jusqu'à ce que l'algue se soit accrochée. Ou bien, il l'accroche sur la surface externe des pattes ambulatoires, également munies de crochets, en approchant la patte et en la pliant sous la face ventrale de la carapace.

"Les procédés sont identique, si l'on fournit aux crabes, à la place des algues, des éponges, des hydaires ou des ascidies composées S'ils ne trouvent pas des matériaux vivants ils se contentent de débris, de morceaux de carapace de crustacés morts, de coquilles, de tout ce qu'ils trouvent enfin: du papier, des chiffons, des fils, etc."

The author has only to add that in the disguising or decorating of posterior portions of the carapace, the two posterior walking legs, in working upon the posterior portions of the carapace, play a part similar to that of the chelipeds except that, naturally, they are not able to prehend the object. The bit of alga, etc., is placed upon the extreme posterior portion of the carapace by the chelipeds. The right or left posterior walking leg extends, rotates medially and flexes in such a way as to bring the pointed terminal segment of the leg down upon the alga and by a sort of prodding movement affixes it to the carapace. In addition to the act of decoration, the crabs occupy themselves much with a kind of activity which suggests strongly the "preening" habits of birds. While thus engaged, the crab remains in the same place. The maxillipeds and the chelae are restlessly active. The chelae explore the dorsum of the carapace, grasp hairs and strip them lengthwise of whatever may be upon them. The result attained by these acts may be a cleansing.

The problems which are suggested by a study of the disguising reactions of the crab may be grouped as follows:

(1) By what means or instruments are the foreign bodies made to adhere to the body of the animal;
(2) By the action of what stimuli and by the execution of what responses is the disguising brought about;
(3) What end is sought, what purpose is served or what *telos* is realized by the series of reactions which results in a disguise.

The third of these questions may, from the author's point of view, be disposed of most easily. If the question means that the crab seeks some end of which it has any consciousness, or that the animal carries out a purpose of which it is dimly aware, the answer is that the crab seeks no end and carries out no purpose. Both end and purpose exist only for the anthropomorphizing human observer. From the point of view of such an observer, the crab does disguise itself, if to disguise means to alter the normal appearance of the body by the addition of objects which are foreign to it. The change of appearance in the body of the crab is the same to a human observer as would result if the animal were actuated by motives similar to those of a human individual consciously seeking to change his appearance with a wig and paint. Furthermore, the supposed "choice" of materials of the same color as that of the environment which Minkiewicz claims to have demonstrated, although all other observers have failed to confirm this result, may be explained upon the ground that in the natural habitat, the prevailing color of the environment is due to the most abundant material which, consequently, the crab meets with most frequently. Under the conditions which exist upon the littoral of the sea where the prevalent color tone is due to the most abundant material, the appearance of a harmony between disguise and environment results, which can not be confirmed under experimental conditions. Thus the purposiveness of this "harmony" turns out to be, like the purposiveness of the disguise itself, illusory.

In the experimental work about to be described, the effort was made to answer the first two questions.

II. EXPERIMENTS

The experiments were carried out during the summer of 1912 at the Puget Sound Marine Station, Friday Harbor, Washington.[6] Seven genera of the Majidae are found in the waters of Puget Sound: Hyas, Epialtus, Chorilia, Chionoecetes, Scyra, Pugettia and Oregonia. All seven forms (with the possible exception of Chionoecetes) show some tendency towards protective concealment, although the instinct is most marked in Oregonia gracilis which locally is known as the decorator crab.

[6] A systematic study of the plants and animals found upon Oregonia gracilis has been undertaken by Miss Evelyn Way under the supervision of Professor Trevor Kincaid, Director of the Puget Sound Marine Station. With their permission, the following incomplete list of plants and animals is here given to convey to the reader some idea of the variety of material found upon this crab.

PLANTS

Ulva
Polysiphonia pennata
Polysiphonia bipennata
Antithamnion
Antithamnion americanum
Kelp
Callithamnion
Ceratothamnion pikeanum laxum
Callophyllis flabellulata
Ectocarpus
Platythamnion heteromorphum
Pleonosporium vancouveranum
Nitophyllum latissimum
Dasyopsis plumosa
Bryopsis plumosa
Monostroma
Cladophora
Mesogloia andersoni
Desmarestia aculecata
Desmarestia ligulata
Dichtoniosiphon
Delessaria
Laminaria
Ceramium rubrum
Apoglossum
Fanchea gardneri
Iridea
Pterisiphonia dendroidea
Diatoms
1. *Navicula grevillei*
2. *Licmophora flabellata*

ANIMALS

Hydroids
1. *Hydractinia aggregata*
2. *Clytia edwardsi*
3. *Perigonimus repens*
4. *Tubularia harrimani*
5. *Abelaria gelatinosa*
6. *Abietinaria trashi*
7. *Sertularella tricuspidata*
8. *Plumnlaria setacea*
9. *Selaginopsis mirabilis*
10. *Thuiaria similis*
11. *Abietinaria variabilis*
12. *Aglaophenia struthionides*
13. *Lafoea dumosa*
14. *Lafoea gracillima*
15. *Campanularia regia*
16. *Sertularella polyzonias*

Sponges
1. *Grantia sponge*
2. *Volcano sponge*
3. Six other varieties not identified

Anemones

Tubeworms

Barnacles

Little blue mollusc (*Mytilus edulus*)

Tunicates

Seamats

Mollusc eggs

Little white sea cucumbers

This species alone was used in our studies. These studies were aimed at a solution of the following problems:

1. The color reactions of crabs which have been exposed to white light.
2. The color reactions of crabs which have been exposed to colored light.
3. The influence of the color of the environment upon the color of the material which is used for decoration.
4. The effect upon the disguising instinct, of blinding the crabs.
5. The orientation of blinded crabs to light.
6. The function of the dorsal hairs.

All reactions to color were carried out in a light-proof reaction box which was 45 cms. in length, 30.5 cms. in breadth, and 17.5 cms. in depth. Two windows 8.5 cms. by 11 cms were cut in one end of the box. A partition 10 cms. by 17.5 cms. was nailed to the bottom of the box midway between the two windows. At the opposite end of the box, a V-shaped pen was made by nailing a strip of wood 10 cms. wide by 17 cms. long perpendicularly to the floor of the box and so placed as to bisect the corner angles of the box. An opening 5 cms. in breadth was left at the apex of the pen and on the side towards the source of light. Colored lights were obtained by placing colored glasses or filters in the windows which have already been mentioned. See Figure 1 for a plan of the box. A square hole, large enough to admit the head of the observer, was made in the lid. Light was excluded by means of a hood of cloth.

The sources of light were three glasses and two filters. The glasses were ruby red, a green, and a colorless glass. The color analyses and spectral transmission of these glasses were made by the Bureau of Standards of the United States Government. These analyses are given below. According to a statement made by the Director of the Bureau of Standards, "The properties of the clear glass are so nearly those of absolutely colorless glass that we have not undertaken the very expensive investigation that would be necessary to determine them." The yellow light was obtained by means of a potassium dichromate solution (10 gms. to 300 cc. of distilled water) contained in a flat-sided glass filter the cubic dimensions of which were

approximately 10 x 16 x 3 cms. The glass walls of the filter were 5 mm. in thickness. Blue light was secured by an ammoniacal solution of copper sulphate (10 gms. of copper sulphate to 300 cc. of water plus 10 cc. of ammonia). This solu-

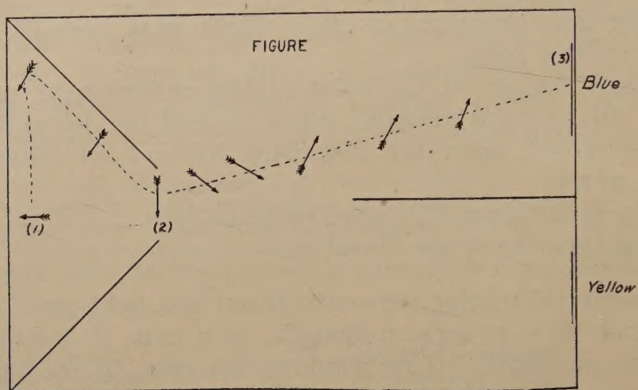

Figure 1 shows the reaction of Specimen 12 (VIII-25-1912, 12.30 P. M.) to blue and yellow light. The head of the arrow indicates the head of the crab. The dotted line indicates the path. The time spent in moving from (1) to (2) was 25 seconds; from (2) to (3) 10 seconds.

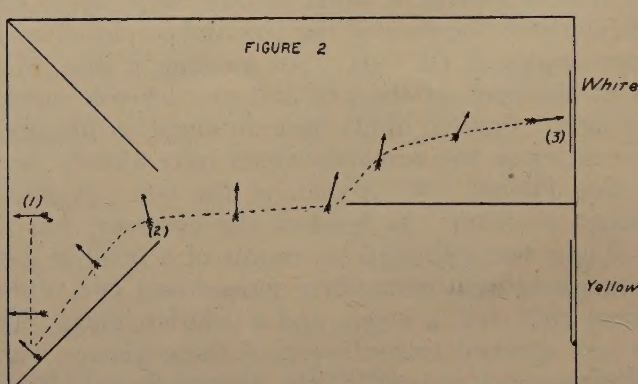

Figure 2 represents the reactions of the same crab as shown in Figure 1. The time spent in moving from (1) to (2) was 30 seconds; from (2) to (3) 20 seconds.

tion was placed in a filter similar in form to that which contained the solution of potassium dichromate. The tops of both filters were covered with a glass plate and sealed with balsam.

The color analyses and the spectral transmission of the lights as determined by the Bureau of Standards are here given:

Color Analysis

	Dominant Hue	Per Cent White	Total White Transm.
Green glass	540	47	39.6%
Red glass	650	26	1.3
Yellow liquid (1 cm.)	584	18	51.2
Blue liquid (1 cm.)	468	45	14.1

Spectral Transmission

Wave Length	Red Glass	Yellow Liquid 10 mm.	Green Glass	Blue Liquid 10 mm.
430 $\mu\mu$	0.0	0.0	5.2	69.9
40	0.0	0.0	7.9	64.8
60	0.0	0.0	24.2	52.2
80	0.0	0.0	41.8	30.6
500	0.0	0.0	59.8	30.6
20	0.0	0.0	68.0	16.0
40	0.0	36.0	62.9	7.6
60	0.0	80.8	48.3	3.4
80	0.5	90.5	35.6	1.8
600	1.4	95.0	27.1	1.2
20	6.4	96.8	18.0	1.2
40	16.4	97.3	12.7	1.2
60	26.5	97.1	10.4	1.7
80	34.6	97.0	8.5	2.2
700	42.1	97.1	7.9	3.4
20	44.7	97.1	7.0	4.9
40	45.0	97.1	7.4	6.6

The reaction box was attached to the wall of an aquarium which floated in the Sound. This aquarium was about 160 cms. in length by 120 cms. in breadth by 60 cms. in depth. The long dimension of the aquarium was approximately northeast by southwest. The reaction box was attached by its long side to the southeast wall of the aquarium with its two windows facing the northeast. The box was submerged to a depth of 12.5 cms. Inasmuch as the experiments were made for the most part in the morning at approximately the same time (from 9 a. m. to 11 a. m.) a certain constancy of illumination was secured. The specimens were collected from time to time as they were needed. When not being used for reactions they were placed in the aquarium above described. This aquarium proved to be very suitable for marine plant and animal life as very delicate deep-sea forms throve in it for weeks at a time. The attempt was made to secure reactions to light from the crabs when the box was out of the water. These attempts proved unsuccessful. The reaction box was therefore submerged to the depth already mentioned which was sufficient to cover the windows. In this way, the intensity of the light was cut

down by a constant but unknown amount. When the head of the observer was introduced into the opening in the lid of the box and all light excluded by means of the hood, the only sources of light were the two windows which appeared brightly illuminated. Even with the least bright colors, red and blue, with dark adaptation of the eyes of the observer, the movements of the crab could be seen.

In the study of the reactions to light, the mode of orientation of the animal and its final position with reference to the source of light were observed and two times were measured. The two times were those which elapsed from the moment when the crab was placed in the V-shaped pen until the moment it emerged from the pen; the other time was that which elapsed from the moment of emergence from the pen until the source of light was reached. See Fig. 2. Inasmuch as the crab is an exceedingly thigmotropic individual, the length of time which passed in the pen before emergence was very variable. On the other hand, the time between emergence from the pen and the reaching the source of light, which I shall speak of as the reaction time to light, was much more constant, although subject to considerable variation both with respect to the lights and to the animals used. The times of emergence from the pen and the attainment of the light were signalized by the observer whose head was in the reaction box by snapping the fingers. An assistant outside who held a watch recorded the time. The movements of the crabs are very deliberate so that the second is a sufficiently small unit in which to measure the reaction time. In the study of the orientation of the animal each change of position, from the position in which it was placed in the pen, until it reached the source of light, was recorded by the observer upon a diagram of the interior of the reaction box. A record was thus kept of each crab's route as it passed from the pen to the windows.

Under the conditions of the experiments two variable factors entered into the behavior of the crabs in such a way as to modify their reaction times and their modes of orientation. These factors were thigmotropism or its more special form of "goniotropism," as Minkiewicz calls it, and habituation. At the beginning of a reaction experiment, the crab was placed in the middle of the V-shaped pen with its cephalothorax away from the source

of light and the mid-line of its body coinciding with the middle line of the reaction box. With only one or two exceptions, the first movement of the animal was towards the rear wall of the pen, then to right or left to the corner of the box. On reaching the corner, the animal usually turned to right, if it occupied the right corner, (the observer is supposed to be facing the windows) or to the left, if it occupied the left corner in such a way that long axis of its body was perpendicular to the oblique partitions of the pen and the walking legs on one side of its body in contact with the rear wall of the box. On moving out of the pen, progress was always a sort of sidewise sidle along the oblique partition of the pen, with the long axis of the body perpendicular to the wall and the walking legs of the side exposed to the light reaching out along the floor and wall. On emerging from the pen, the long axis of the animal's body was transverse to the long axis of the box, but exactly on the middle line of the box. One side of the crab was, therefore, exposed to the action of the light from the two windows. Since the oblique wall of the pen made an angle of about 45 degrees with the side of the reaction box, it is evident that the long axis of the crab must have rotated through an angle of 45 degrees before it could become transverse to the long axis of the box. Such a rotation did actually take place when the crab arrived at the end of the oblique partition. The posterior walking legs on the side towards the light would reach around the end of the partition and swing the body of the crab into a position at right angles to the long dimension of the box. In very rare cases when the crab was very weakly positively phototropic, the movement of rotation would continue until the animal was completely outside the pen but still in contact with the partition, the long axis of its body perpendicular to the partition, as ever. In these rare cases, the animal would sometimes continue its side-wise progress until it occupied the corner at the rear of the box between the oblique partition and the side. In the typical reaction of a majority of positively phototropic crabs, the animal, on emerging from the pen, struck out without hesitation along the middle line of the box until it reached the medial partition between the two windows. Upon contact with the partition, rotation would occur, sometimes with a slight hesitation, usually, however, without, and the animal would

continue into the open space, exclusively lighted by one of the windows. It is to be noted that up to the time that the middle partition is met with, locomotion is in a side-wise direction, with reference to the long axis of the crab's body. On orienting to the light, after coming in contact with the partition, rotation occurs about the posterior mid-point of the carapace, in such a way that the anterior end of the animal is directed towards the light. As the crab moves towards the light, with the long axis of its body obliquely disposed with reference to the length of the box, as a result of the rotation just described, further rotation of the long axis of its body with reference to the long axis of the box takes place, with the result that the anterior end of the body is turned directly towards the source of light and both sides of the body are equally illuminated. This type of orientation is shown in Fig. 2. This rotation of the body so that the light fell equally upon both sides, was very striking with the white and green glasses. With red it was least. Blue probably stands next to red in this respect, with yellow next to green. In a considerable proportion of the reactions, the crabs, upon emerging from the pen, rotated towards the light (from the transverse position with reference to the mid-line of the reaction box, which they always occupied on leaving the pen, to the right or left according as the head was pointed to the left or right), immediately, without advancing to the partition in the manner which has just been described, and struck out in an oblique direction towards the right or left source of light. This type or orientation is shown in Fig. 1. As the animal advanced towards the light, the anterior end turned more and more as the window was approached, until, when it arrived, both sides were equally exposed to the light. An analysis of the reactions has been made with view to finding out what proportion of the reactions ended in the manner just described and what sort of glass caused such reactions. Out of a total of 105 reactions in which the head was directed towards the source of light with each side of the body equally exposed to it, 47 were reactions to white, 24 to green, 17 to yellow, 14 to blue and 3 to red, light. Without entering into a discussion of theories at this point, it may be pointed out that these results seem to show that unequal intensity of stimulation of the two sides of the crab's body is the chief factor in orientation.

In describing the manner in which the crabs behave after being released in the pen with the anterior end facing towards the rear of the box, it was stated that some of the animals moved to the left and some moved to the right corner of the pen. It was shown, furthermore, that the animal sidled along the oblique partition of the pen and finally emerged with the longitudinal axis of its body transverse to the mid-line of the box and with its cephalothorax pointing either to the right or left, so that the right or left half of the body only was exclusively stimulated. The question naturally arises whether the side of the body (right or left) which is exposed to the light influence to any extent the window (right or left) to which the animal reacts. An analysis of the reactions with respect to this point shows that out of 198 reactions, the crab emerged from the pen with the head towards the right side of the box, 63 times. Of these 63 reactions, 31 reactions were to the light in the *right* window, and 32 reactions to the light in the *left* window. The distribution is exactly what one would expect if chance alone were operative. In 135 cases the crab emerged from the pen with the head directed to the left side of the box. Of the 135 cases, 72 went to the *left* light and 63 to the *right* light. Although the figures show an excess of 9 in favor of the left window, the author considers this only such a deviation from the distribution according to chance as is to be expected from a small number of reactions. On the other hand, the head upon emergence from the pen was turned to the right in 63, and to the left in 135, cases. This difference is too great to be attributed to chance. Some influence must have been at work to determine the predominance of the reactions with the head towards the left. This influence might conceivably be resident in the reaction box itself, in the crab or in some circumstance outside of the box. As far as could be seen, the right and left sides of the box were exactly alike. So far as is known the two sides of the body of the crab are identical. Of the circumstances existing outside of the box, there is the fact that the observer sat upon the right side of the reaction box. It seems likely, therefore, that the observer in some unknown manner, either in placing the crab in the pen or by the mere presence of his body upon the right side of the box, influenced the initial turning of the crab.

The other general factor, besides thigmotropism, which influenced orientation was habituation to the reaction box. Inasmuch as five different stimuli were used, it is evident that each compared with every other gives 10 combinations. Since each stimulus was presented first upon the one side and then upon the other, the total number of reactions for the five lights was twenty for each crab. The usual order of the reactions is shown in Table I. With an animal which reacted tolerably briskly, a series could be completed in one hour. With most crabs, however, the time was much longer for the reason that the animal seemed to become habituated to the conditions existing in the box. The first few reactions were usually rapid. As the series lengthened, however, the duration of the time spent in the pen increased, until in many instances the work had to be abandoned for that particular day.

TABLE I

Shows the Order in which the Colored Lights were Exposed in the Reaction Box, the Numbers Indicate the Number of the Experiment in the Series. The Right or Left Position of the Figure in the Column Indicates the Right or Left Position of the Color at the Top of the Column. Thus Experiment 6 in the Table Means that Red was Presented on the Right side of the Reaction Box with Blue on the Left.

	R		Y		G		B	
Y	1	2						
G	3	4	9	10				
B	5	6	11	12	15	16		
W	7	8	13	14	17	18	19	20

1. *The color reactions of crabs which have been exposed to white light.*—Ten specimens of Oregonia gracilis were used, the sex and number of which are given in the following table. The five lights, with the general arrangements already described, were presented in pairs with an exposure of each color upon the right and left sides. A complete series consisted, for each individual, of 20 reactions, arranged as shown in Table I. This number was secured for every crab except Specimen 9 whose series consists of 18. Although this animal was exposed to the action of the blue and white lights on four successive days,

(September 2, 3, 4 and 5) no reaction was obtained. Counting each reaction for each animal as an observation, the total number of observations under these conditions was 198. The distribution of the reactions with respect to each light and to each crab is given in Table II. The letters L and R indicates whether the light occupied the left or right window of the reaction box.

TABLE II

	Red		Yellow		Green		Blue		White		
Specimen	L	R	L	R	L	R	L	R	L	R	Total
3 ♀	0	1	1	1	4	3	2	2	3	3	20
4 ♀	1	0	3	2	2	2	0	2	4	4	20
7 ♀	0	0	1	2	2	2	3	2	4	4	20
8 ♀	0	0	1	3	3	2	2	1	4	4	20
9 ♂	0	0	2	2	3	2	2	2	2	3	18
12 ♀	0	0	2	2	2	1	2	3	4	4	20
13 ♀	2	0	0	2	3	2	1	2	4	4	20
14 ♀	2	1	1	1	2	2	2	2	3	4	20
15 ♀	0	1	2	2	3	2	1	2	4	3	20
16 ♀	2	3	3	0	1	1	0	2	4	4	20
	7	6	16	17	25	19	15	20	36	37	
Total	13		33		44		35		73		198

It will be seen from the table that the white light received most of the reactions, with green next, then blue and yellow about equal, and finally red least of all. The table also shows in which window (right or left) the light was exposed when it was reacted to positively. It will be seen that with red, yellow, and white the reactions were divided about equally between the right and left windows. With green there is an excess of 6 in favor of the left window; while with blue there is an excess of 5 in favor of the right window. The author considers these deviations from the distribution according to chance, to be non-significant, although he is unable to account for them. Figure 3 shows by means of a graph the distribution of the reactions with respect to lights, which are exhibited in Table II.

The reaction times of the ten crabs which were used in this set of observations have been determined and grouped. The time measured was the time in seconds which elapsed between the emergence of the animal from the V-shaped pen and the

attainment of the window. The individual reaction times for each light and for each specimen are shown in Table III. The numbers mean number of seconds.

2. *The color reactions of crabs which have been exposed to colored lights.*—The object of these experiments was to determine whether Oregonia gracilis possesses a chromo-kinetic resonance in the sense in which that term is used by Minkiewicz. The experiment upon which Minkiewicz bases his conclusion that a chromo-kinetic resonance exists is described by him in the following passages. "On met les crabes dans les aquariums préparatoires, chacun d'une couleur différente et ne contenant que du matériel de déguisement de la même coleur. On divise

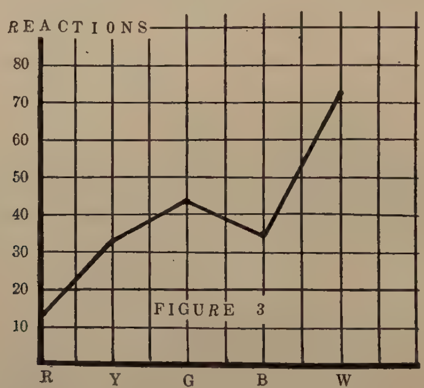

FIGURE 3 represents the distribution of the reactions with respect to lights.

un autre aquarium en deux moitiés diversement colorées et on y transporte les crabes une fois revêtus dans les aquariums prêparatoires.

"On voit alors, les crabes se diriger constamment vers la moitié de l'aquarium dont la couleur correspond à celle du papier de leur revêtement et y rester pendant longtemps. Ainsi, par example, dans l'aquarium rouge-vert les crabes rouges se dirigent vers le milieu rouge, les crabes verts vers le milieu vert.

"L'expérience la plus frappante était celle faite dans l'aquarium divisé en trois partie égales, dont la médiane était colorée en blanc, les deux autres en noir. Les crabes blancs gagnèrent la partie médiane (blanche) et restèrent là pendant toute la durée de l'expérience (quelques heures). L'expérience de con-

TABLE III

Shows the Duration and Distribution of the Reaction Times for Each Specimen and for Each Light

Specimen	R	Y	G		B	White	
3	70	15 19	50 10 36 150	145 55 80	33 15 27 24	37 60 20	60 27 16
4	30	10 10 10 40 55	17 25 35 7		10 15	10 20 10 8	11 5 8 10
7	0	20 90 25	30 30 20 25		16 10 10 30 15	15 20 25 15	15 22 15 15
8	0	25 40 10 10	35 7 12 10	5	5 10 60	9 15 5 35	20 5 15 10
9	0	15 40 5 65	45 75 90 8	240	40 135 15 300	255 5 20 5	65
12	0	15 40 10 5	25 20 15		10 30 10 25 10	10 20 10 20	20 25 15 20
13	10 147	3½ 4	7 3 7 10 4		40 18 5	7 7 10 50	11 13 10 8
14	16 12 42	14 8	55 7 12 10		23 80 8 10	9 9 8 12	7 8 9
15	15	15 12 20 34	22 40 27 15	9	15 34 17	21 25 28 21	12 50 15
16	13 56 188 15 13	8 13 240	13 35		23 33	10 10 31 24	34 53 62 36

trole dans l'aquarium blanc-noir-blanc me donna le même résultat pour les crabes noirs."[7] The "choice" of costume is thus explained.[8] "L'animal mis dans un milieu coloré—vert, par example—en acquérant sous l'influence directe du milieu, par résonnance chromo-cinétique, le chromotropisme correspondant (synchrome), devient *chlorotrope* et par conséquent négatif vis-a-vis des autres couleurs. S'il trouve des papiers de couleur, il ne peut prendre, c'est-a-dire s'approcher, ni des rouges ni des blancs, etc., ces couleurs faisant dans l'aquarium vert des surfaces négatives (repoussantes) pour l'animal accordé chlorotropiquement. Or, il se déguisera en vert, qu'll rencontrera en errant sur les surfaces verts. * * * Il en est de même dans un milieu de n'importe quelle couleur excepté le milieu de noir." Minkiewicz here contradicts a statement which is made in the first of the two citations where he says "L'expérience de controle dans l'aquarium blanc-noir-blanc me donna le même resultat pour les crabes noirs." Briefly put, Minkiewicz's doctrine states that the light receptor system of the crabs, together with their central connections, acquire, by exposure to light of a certain wave length, a specific sympathetic, resonance (synchrone resonnance). By virtue of this specific, sympathetic, resonance, ambulatory movements are initiated which are specific, in the sense that they carry the animal fatally towards the source of light of the same wave length as that to which it has been exposed. Hence the chromo-kinetic-resonance. To obtain experimental evidence upon this subject, a series of observations was made in which certain crabs were exposed to different colored lights for a period of time from 24 to 36 hours in length. It was assumed that such a period was sufficient for the animals to acquire the chromo-kinetic resonance, if such exists. After exposure to the action of the lights, for the times stated, the crabs were placed in the reaction box and their reactions to a series of lights, presented two at a time, one of which was the light to which the animal had been exposed, were determined. The lights used in the reaction box were those used in the experiments already mentioned. The colored light to which the crab had been exposed was presented with each of the other four lights, first on the right, and then on the

[7] Analyse Experimentale, p. 41.
[8] Ibid., p. 54.

left, side. Eight reactions were thus obtained, in which the animal was given the opportunity to react either to the color to which it had been exposed or to another. Although one color was thus exposed 4 times to once of each of the other colors, it is the author's opinion that the results are not vitiated by this procedure. Evidence for this position is furnished by the reactions of Specimen 16, from which a complete series of 20 observations was obtained. Although this individual was exposed to the action of red light for 24 hours prior to the reactions, a marked chromo-kinetic-resonance is apparent which is not altered in any way by the subsequent reactions to the other lights. It seems reasonably certain therefore that had a full series of twenty reactions been obtained from each of the other specimens which had been exposed to a certain light, the results would not have been different from those actually obtained. Furthermore, as appears from Table I, which shows the order in which the lights were presented, in the experiments recorded in Table II red was shown 8 times, yellow 6 times, green 4 times and blue 2 times in succession. Yet in spite of the inequality in the order of presentation, there is no evidence whatsoever that the light which was exposed most often in succession, received most reactions. In fact red which heads the list in this respect, was reacted to least frequently. The results which follow, therefore, can not be explained upon the assumption of an undue influence of the color from the frequency of its successive presentation.

The aquaria in which the crabs used in this series were exposed to colored light for 24 hours prior to testing their reactions in the manner just described, were made by painting the insides and bottoms of galvanized iron pails. The diameter of the top was 250 mm. that of the bottom 212 mm. The depth of the pails was 250 mm. The area of the sides and bottom is equal to 2063.85 sq. cms. The color of the paints can not be characterized very definitely. The red was a vermilion; the blue an ultramarine; the green a "dark" green; the yellow a "lemon" yellow. The aquaria were suspended in the large aquarium already described, in such a manner that their tops were about 3 cms. under the surface of the water. In this way, a supply of fresh water was secured. The observations in the reaction box were made immediately after taking the animals

from the colored aquaria. The procedure of these experiments was exactly the same as that already described. The general type of orientation, the effects of thigmotropism and habituation, the length of the reaction times were about the same as those described above. The results of these experiments are shown in Tables IV, V, VI and VII; and their corresponding Figures, 4, 5, 6 and 7. Each centimeter of the cross-section paper indicates one reaction.

TABLE IV

Shows the Reactions of Individuals which Had Been Exposed to Red Light

Specimen	R	Y	G	B	W	Total
21 ♀	1	2	2	1	not used	6
16 ♀	5	1	0	0	2	8
	6	3	2	1	2	14

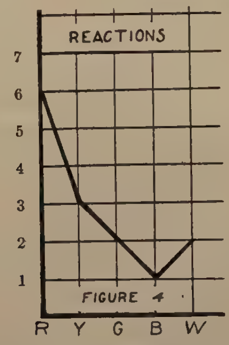

Figure 4. Shows the curve of distribution of the reactions of Table IV

It appears to be very certain, judging from the results of these experiments, at least, that the color reactions of *Oregonia gracilis* are influenced in a dominant degree by the color of the light to which the crab is exposed. The curves show clearly that the maximum number of reactions invariably falls to the colored light of the same quality as that to which the animal has been previously exposed. Of the ten specimens used in this series only two, Specimens 18 and 21 failed to react maximally to the light to which they had previously been exposed.

With the other eight crabs, the majority of the reactions fall to the colored light used in the preparatory stimulation. There exists, therefore, very strong, although not absolutely conclusive, evidence that *Oregonia gracilis* acquires by exposure to the action of colored lights, a specific chromotropism for the light thus used.

TABLE V

Shows the Reactions of Individuals which Had Been Exposed to Yellow Light

Specimen	R	Y	G	B	W	Total
22 ♀	0	3	2	1	2	8
23 ♀	1	3	2	0	2	8
	1	6	4	1	4	16

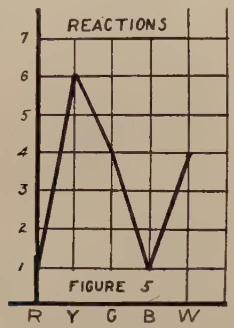

Figure 5. Shows the curve of distribution of the reactions of Table V

TABLE VI

Shows the Reactions of Individuals which Had Been Exposed to Green Light

Specimen	R	Y	G	B	W	Total
17 ♀	1	1	3	1	2	8
18 ♀	2	1	1	2	2	8
19 ♂	1	1	4	1	1	8
20 ♀	1	1	2	not used	not used	4
	5	4	10	4	5	28

3. *The influence of the color of the environment upon the color of the material used in decoration.*—The experiments of this section were devised to determine whether the color of the material used by the crab in decoration bore any direct relation to the color of the environment. The same four colored aquaria as were used in the experiments upon the chromokinetic resonance were employed here. The colors were red, yellow, green and blue. A black aquarium was added, as it was stated by Minkiewicz that the animals do not decorate themselves in black aquaria. The general plan of the experi-

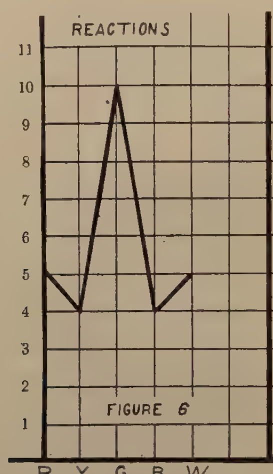

FIGURE 6. Shows the curve of distribution of the reactions of Table VI

ments consisted in carefully stripping off all detachable decorations from five individuals and placing each of them in one of the colored aquaria. Colored tissue papers of the same dimensions were also placed in the aquaria. The animals were left in the aquaria for a period of several hours, usually over night. Three series of experiments, in which five different crabs were used in each series, furnish the evidence upon which our conclusions are based.

First Series

IX–3–1912. 12:30 P. M. Five individuals were carefully cleansed of all algae, hydroids, etc. Ten pieces, 5 x 5 mm., of each of five colored papers were placed in the aquaria. The

colors of the papers were red, yellow, green, blue and black. These papers were not standardized with reference to any code. Results: At the end of 36 hours, no individual had used any piece of paper for decoration. During the time that the crabs were under observation, they moved about the bottom of the aquarium, trying vainly to escape. At times they remained

TABLE VII

SHOWS THE REACTIONS OF INDIVIDUALS WHICH HAD BEEN EXPOSED TO BLUE LIGHT

Specimen	R	Y	G	B	W	Total
24 ♂	0	0	2	4	2	8
25 ♀	1	0	1	4	2	8
	1	0	3	8	4	16

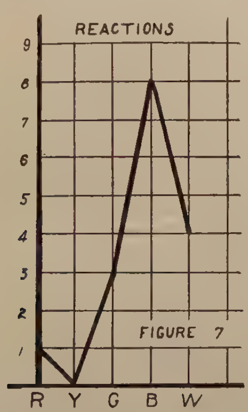

FIGURE 7. Shows the curve of distribution of the reactions of Table VII

motionless and busied themselves with "preening" their hairs. They seemed not to notice the presence of the paper.

Second Series

IX–9–1912. 5 P. M. Five crabs, two males and three females, were carefully cleansed of all decoration and placed in the aquaria. Five pieces, 10 x 10 mm., of each of five colored papers were placed in the aquaria. A piece of dead clam was also added. The animals ate voraciously and "preened" themselves.

Results: IX–10–1912. 3:30 P. M. Red aquarium. Male. Crab was alive. Not decorated, although ulva had floated in. Yellow aquarium. Female. Animal alive. Decorated with green ulva which floated in during the night. Green aquarium. Female. Animal alive. No decoration, although ulva had floated in. This was 10.30 A. M: Cleaned out aquarium and placed in it two new individuals carefully cleansed. At 3:30 P. M. same day, there was no decoration. Blue aquarium. Male. Crab alive. Not decorated. Black aquarium. Female. Animal alive and gaily decorated with torn pieces of the colored paper. There were six pieces of green, four of blue and two of yellow. No crab ever made use of the papers to the extent of this individual. Killed IX–11, 1912 and preserved in formalin.

Third Series

IX–11–1912. 5:30 P. M. The five aquaria and five crabs carefully cleaned. Five strips, 10 x 60 mm., of each of the five papers were placed in the aquaria. Results: 9 A. M. IX–12–1912. Red aquarium. Female. Animal alive. Not decorated. Yellow aquarium. Female. Animal alive. Not decorated. Green aquarium. Male. No decoration. Animal alive. Blue aquarium. Female. Animal escaped. Black aquarium. Animal alive. Decorated with a large piece of red paper on its rostrum and an entire strip of blue paper on its carapace. Preserved [9] in formalin IX–12–1912. 10 A. M.

The chief conclusion to be drawn from these experiments is that these crabs do not decorate themselves with materials of the same color as the color of their environment. Our experiments therefore support the results of Pearse, Mast and others who have carried out similar experiments upon *Libinia emarginata.* One is surprised at the prevalence of the view that these animals "choose" colors of the same color as their environment, when the evidence upon which this view depends for its support is critically examined. Minkiewicz is the only experimenter who has given assent to the doctrine of selective, protective, concealment. And while he attempts to explain the reactions which result in concealment in a purely mechanical

[9] Formalin was unfortunately chosen as the preserving fluid. It was hoped that individuals might be preserved for demonstration purposes with all their regalia on them. The action of the formalin, doubtless as a result of the aldehyde, has almost completely bleached the colored papers.

manner, which as a general mode of explanation of animal behavior is entirely acceptable to the writer, the experimental work upon which Minkiewicz bases his conclusions has never, to the knowledge of the present writer, been satisfactorily presented in any scientific journal. Without exception, Minkiewicz's experiments have been stated in a general form so involved in theoretical considerations that the facts themselves ascertained by experiment have never received proper attention. Until Minkiewicz publishes the actual results of his experiments and not the inferences which he wishes to draw from them, his scientific colleagues will be justified in accepting the alleged results with reservation.

A second conclusion which can be drawn from our results is that the size of the paper placed in the aquarium has a distinct effect upon the use of the paper for decoration. With bits of paper 5 x 5 mm. no decoration at all occurred. With the larger pieces decoration resulted in both cases. In view of the results obtained from the blinded crabs it seems likely that the stimulus to the decorating instinct is tactile. Those pieces of paper sufficiently large to catch upon the chelae of the crab excite the decorating response. Those pieces, like our 5 x 5 mm. pieces, which are so small and tenuous as to give no adequate stimulus to the claws of the crab, are passed over unnoticed.

4. *The effect of blinding upon the decorating instinct.*—Early in the experiments, the attempt was made to determine by means of an *experimentum crucis*, the rôle played by the eyes in the decorating reactions. On the assumption that the reactions were responses to visual stimuli, for on no other assumption could the supposed harmony between the color of the decoration and the color of the environment be explained, the elimination of the eyes would abolish the response, unless some other stimulus than visual, could set off the instinct. If some other than a visual stimulus could initiate the response, the resulting decoration ought to bear no relation to the color of the environment, unless the crab possesses color-sensing organs other than the eyes. The result of the next section on the reactions of blinded crabs to light, may be anticipated to the extent of stating that no evidence exists to show that blinded crabs react to light. The eyes therefore are the exclusive light receiving organs. The results with the blinded crabs show that

a tactile stimulus may initiate the decorating response. There is, however, no evidence to show that the tactile stimulus is the only stimulus adequate to produce this response. Whether visual stimuli alone may initiate such responses is as yet undetermined. Complete tactile anaesthesia would be necessary with vision unimpaired. Such an experiment is technically feasible and ought to be made forthwith.

Four crabs were used in this experiment. Specimen 7, a female, was blinded VIII–21–12 by cutting off the eye stalks close to the orbit by means of a pair of scissors. The animal was then placed in the aquarium. It manifested considerable restlessness by moving about the walls of the aquarium. It assumed a position in one corner of the aquarium from which it refused to move for some time. On VIII–28–12 this individual was found to be gaily decorated with ulva. These decorations were removed completely and on the next day, VIII–29–12, the animal was observed to be again decorated with seven or eight pieces of ulva which had been placed upon the legs and back of the carapace. The animal was observed from time to time until IX–6–12 when it was found to be covered with polysiphonia with only two pieces of ulva on the legs. The polysiphonia had been placed in the aquarium VIII–27–12. No other crab made use of this material for decoration. The polysiphonia was removed from this individual IX–6–12. Nothing had been added by IX–8–12, 12:30 P. M. The animal died IX–9–12.

Specimen 26, a young female, was blinded IX–7–12 at 4 P. M. by cutting off the eye stalks with a pair of scissors. All foreign material was then stripped off from the carapace and legs by means of a pair of forceps. Immediately following the operation the animal was very restless and made no attempt either to feed or to decorate itself or to preen. There was no decoration IX–8–12. On IX–9–12 the animal was observed to be covered with pieces of ulva and polysiphonia. The ulva was removed from the rostrum. A few minutes later the animal was observed to place a flag of ulva 18 mm. by 6 mm. on the rostrum after "mouthing" it. The animal was observed to feed on dead clam. On IX–10–12, 2:30 P. M., the animal was observed in the act of decorating itself. The manner of decora-

tion is precisely the same in the blinded crab as in those which have eyes.

Specimen 27, a female, was blinded by cutting off the eye stalks on IX–9–12. Her decoration, which consisted of green and brown algae was carefully stripped off with forceps. The crab was not so restless as Specimens 7 and 26. After the operation the animal remained still with the rostrum toward the side of the aquarium. On IX–10–12, 2:30 P. M., the animal was found to be decorated with polysiphonia and ulva. I observed her at work. She seized a bit of polysiphonia with both claws, tore off a small piece apparently stuffed it into, the "mouth," drew it forth with the right or left chela and placed the weed upon the carapace. If it did not stick the first time she repeated the operation. IX–11–12 the animal was found to be more completely decorated than before with ulva which was placed mainly upon the legs.

Specimen 28, a large male, was very elaborately dressed in green and brown algae with hydroids, small tunicates, sponges and tubeworm on its carapace. After carefully stripping off the decorations with the exception of the tubeworm that could not be removed, the eye stalks were clipped off close to the orbits, IX–9–12. The animal did not appear to be much disturbed. IX–10–12, 2:30 P. M., ~~the~~ animal was decorated with two or three large pieces of ulva upon the carapace. It was observed in trying to place a piece of polysiphonia on the carapace; the polysiphonia failed to stick. The animal did not repeat the operation. IX–11–12, placed a non-mutilated female in the aquarium with this male at 3:30 P. M. At 5 P. M. observed the two individuals copulating. They remained joined for 30 minutes. Called O's attention to them.

The conclusion of these experiments is identical with that reached by Bateson [10] and Minkiewicz.[11] Deprivation of the eyes affects in no particular either the series of acts by which the foreign bodies are applied to the animal's body or the appearance of the resulting decoration.

5. *The reaction of blinded crabs to light.*—In endeavoring to determine the sort of stimulus and receptor which causes the

[10] Notes on the Senses and Habits of Some Crustacea. *Jour. Marine Biological Association.* Vol. I, p. 211, 1889.

[11] Loc. Cit., p. 43. Les Crabes Aveuglés.

decorating response, recourse was had to the experiment of blinding the crabs. It became evident after the experiments, described in section 4 preceding, had been made that a tactile stimulus may serve as excitant to the response. The relation of the response to the visual and tactile stimuli may be represented by means of letters in order to throw more clearly into relief the logical implications of the experiments. Let V stand for the visual stimulus, let T stand for the tactile stimulus, let R stand for the decorating response. In the non-mutilated crab, when R occurs both V and T are present. There are three possibilities as to the relation between R, V and T. V alone may initiate R; T alone may initiate R; or V and T together may initiate R. The experiments with the blinded crabs seemed to show that T alone may initiate R. Whether V alone may initiate R remains to be demonstrated by producing some sort of tactile anesthesia in the legs and chelae without damaging motion. The experiments with blinded crabs seemed to prove beyond doubt that the tactile stimulus alone may initiate the response. Before such a conclusion is warranted, however, the possibility of light receptors other than the eyes must be excluded. It is conceivable that the integument of the crab may respond to light in some such way as does the skin of the frog. To eliminate by experiment this possibility, which indeed seems very remote, blinded crabs were placed in the reaction box and their behavior observed through the hole in the top. Specimens 7, 26 and 27 were used. Specimen 26 gave no reaction whatever when placed in the reaction box with red in the left, and yellow in the right, window. Specimens 7 and 27 wandered apparently aimlessly about the walls of the box without stopping in front of the windows. It seems certain, therefore, that blinded crabs do not react to light stimuli.

III. CONCLUSIONS

1. The color reactions of *Oregonia gracilis* are determined by the color of the light to which it has been previously exposed. This conclusion is justified by the results of section 2 of our experiments. The result may be explained by supposing that this crab possesses a specific chromo-kinetic resonance, or to state the same fact in other words, that it acquires a specific chromotropism. This acquired chromotropism may be as-

sumed to be dependent upon a specific modification of the light receptor organs and the nerve cells connected with them, which determines the kind of stimulus to which a crab possessing such a "resonance" can respond.

2. Blinded crabs decorate themselves as do normal crabs both as regards the mode of operation and the result.

3. Blinded crabs do not react to light stimuli. These latter results taken together show beyond doubt that some other than the visual stimulus may excite the decorating response. This other stimulus may be assumed to be tactile. The results, however, leave in doubt the question whether visual stimuli alone may excite the decorating response.

The results just stated are the only experimentally determined conclusions which may be drawn from our work. And the problem stated at the outset of the paper "By the action of what stimuli and by the execution of what responses is the decoration carried out" must remain unsolved for the present. Of the three possibilities enumerated on page 176 only two, namely, the second and the third can be definitely disposed of. The three possibilities were:

i. Visual stimuli alone may initiate the response.
ii. Tactile stimuli alone may initiate the response.
iii. Visual and tactile stimuli together may initiate the response.

Whether visual stimuli alone can initiate the response remains undetermined by our experiments. It might seem from the existence of a specific, acquired, chromotropism that visual stimuli may certainly excite the instinct in question. Such an assumption is actually made by Minkiewicz. But a moment's reflection will show that all that the chromo-kinetic resonance does is to move the crab fatally towards a source of light of the same quality as that to which it has been exposed. It is quite conceivable that such an acquired chromotropism has nothing whatsoever to do with the decorating instinct. Indeed it is only the belief that a "harmony" existed between costume and color environment that has jutified the assumption. Whether a crab deprived of tactile receptors yet possessing light receptors and impressed with a chromo-kinetic resonance would decorate itself when placed in the presence of suitable material is an unsolved problem. The writer is of the opinion that such an

animal would not decorate itself although he realizes that such a statement is merely an expression of individual opinion.

It seems very unlikely that acquired specific chromotropism is limited to *Oregonia gracilis.* Assuming that the facts stated in section 2 of this paper are confirmed by other workers, it is only reasonable to suppose that similar results will be found in other forms of life. If such a resonance is found to be widely distributed n nature, the co-existence in the same animal of an acquired chromotropism and a decorating instinct would be merely accidental and not causal. Proof by means of an *experimentum crucis*, of this assumed disconnectedness of the two phenomena in *Oregonia gracilis*, depends upon a tactile anesthesia in an animal with a demonstrated acquired specific chromotropism. If such a crab did not decorate itself, the hypothesis here suggested would be confirmed.

RESPONSES OF YOUNG TOADS TO LIGHT AND CONTACT[1]

C. F. CURTIS RILEY

One figure

CONTENTS

I. INTRODUCTION

Several years ago the opportunity arose to investigate the responses of a number of young toads, *Bufo americanus* Le Conte.[2] The toads averaged about 14 mm. in length. The animals were kept in a glass aquarium jar in the laboratory, the vessel being placed 3 m. from an east window in a shaded place. A piece of filter paper, dampened with water, was placed in the bottom of the jar in order to keep the animals moist. They were fed each day on small flies and mosquitoes.

As the toads displayed marked responses to light and contact, it was decided to commence experimentation with photic and contact stimuli. The entire series of experiments were carried on in a dark room at an approximate temperature of 22° C. For experimental purposes, a glass dish with parallel sides was used. The dimensions of the vessel were 60 x 25 x 6 cm., inside measurements. In order to eliminate the effects of reflection, the experimentation trough was painted a dull black on the inside with the exception of the two ends; each of which was covered with a strip

[1] Contributions from the Zoölogical Laboratory, University of Illinois, under the direction of Henry B. Ward, No. 21.

[2] The experimental work was done at Ann Arbor, Michigan, in the summer of 1904, and the first draft of the paper was made the following year. The literature was reviewed, the paper recast and entirely rewritten at Urbana, Illinois, during the winter of 1912-1913.

of paper having a dead black finish. This paper was so arranged that it could be readily removed at either end, thus permitting the rays of light to enter.

Unfortunately, the writer was unable either to complete the work on the responses to photic and contact stimuli, or to commence any experiments on other forms of reaction work. Through an oversight, the water was allowed to dry up in the jar containing the toads, and the next time they were needed for experimentation purposes they were found to be dead. As it was not possible, at the time, to obtain any more material, and as the opportunity to complete the work has not presented itself since then, it was thought best to publish in a brief form the results of the experiments incomplete as they are. The writer hopes, at some future time, to continue the work outlined in this paper in far more detail and to supplement it with experiments on responses to other forms of stimuli.

Thanks are due to Miss F. J. Dunbar of the Zoölogical Department of the University of Michigan, who kindly collected the amphibians used in these experiments. Mr. S. A. Rowland, of the Physics Department of the University of Illinois, calculated the intensity of the illumination within the field of experimentation employed in this work. His assistance is gratefully acknowledged. The writer also desires to express his appreciation of the criticisms and encouragement given by Doctor C. C. Adams of the University of Illinois.

II. RESPONSE TO INTENSE ARTIFICIAL LIGHT

The first experiments undertaken were with reference to intense artificial light as a source of stimuli. The light employed for this reaction work was obtained from the electric arc of a Thomson "90° carbon" projection lantern. The current passed from the electric lighting circuit through a rheostat, and from there to the lantern. The current was direct with an approximate voltage of 210. Within the field of experimentation the illumination was approximately 10,000 ca. m. In order to eliminate the effect of the heat rays, the light was allowed to filter through a cell containing distilled water. Having placed the toads in the glass dish, it was then moved into the beam of light that emerged from the lantern. In order to prevent the organisms from becoming unnaturally dry during

experimentation, the trough was immersed in cool water from time to time, thus keeping the vessel cool and moist.

When the dish is placed in the beam of light, it is noticed that the toads are scattered promiscuously throughout the entire length of the vessel. The first demonstrative movement is a decided orientation. All the animals that are facing the light immediately turn around until their heads are pointing directly away from the source of illumination. The orientation is of such a nature that the longitudinal axes of their bodies become parallel with the rays of light. Those individuals which are facing away from the source of illumination, in the first instance, are already commencing to jump away from the light. After all the toads have completed the orienting reaction, there is a general movement towards that end of the dish farthest from the source of light. The animals jump rapidly toward the extremity of the vessel. The pauses between the jumps are very brief, in many instances barely extending over a second of time. Orientation with the longitudinal axis of the body parallel with the incoming rays is retained while the organisms travel the entire length of the dish. After reaching the end of the receptacle, the toads usually remain oriented with their heads touching the glass. If they are left in this position for some time, many of the individuals climb up the perpendicular end of the vessel as if to move away as far as possible from the source of illumination. Those that climb to the top are not in the most intense glare of the prejection lantern, their elevated position placing them a little above the strong central beam of light. Possibly this movement may be due, in part, to response to contact stimuli. The dish is now turned around until the end where the animals are congregated is again brought nearest to the light. Those animals clinging to the upright end of the vessel quickly drop to the bottom. All the toads promptly perform the reaction of orientation and jump rapidly to the far end of the trough as in the former instance. This reversing of the dish is continued for about eight trials and the animals respond promptly each time to the photic stimuli, the response being as previously described.

Some experiments on the influence of intense light upon the swimming responses of the young toads were also undertaken.

Water with a temperature approximately of 22° C. is poured into the glass receptacle to a depth of 4 cm. The animals are then placed in the water and the vessel moved into the beam of light emerging from the projection lantern. The organisms immediately orient themselves with the longitudinal axis of the body parallel to the rays of light. Complete orientation is quickly followed by every animal swimming vigorously away from the source of illumination to the extremity of the dish. The young toads retain their precision of orientation as they move through the water for the entire length of the vessel. After all the animals have assembled at the end of the dish, it is turned around, thus placing the organisms again nearest the source of light. The animals as before respond promptly, swimming to the far end of the vessel. In this connection it may be mentioned that Torelle (1903, p. 473) while engaged with some very interesting experiments, demonstrated that in water *Rana virescens* and *Rana clamata* move to the illuminated end of a glass trough. Diffuse daylight was used in these experiments.

Many consecutive experiments of the nature of the above were performed, the toads orienting themselves each time in such a manner that the long axis of the body becomes parallel to the rays of light; and they swim away from the source of illumination as already explained. Frequently after reaching the extremity of the glass trough, many of the toads climb up its perpendicular wall. Attention has been drawn to this movement in connection with the responses out of water. The animals respond as if they are attempting to recede as far as possible from the source of stimulation. When the end of the dish, where the toads are congregated, is placed next to the light, they very promptly drop off the perpendicular glass wall into the water. Sometimes there is an attempt at orientation even before leaving the wall of the trough for the water. The results of the experiments in connection with both the jumping and swimming responses of young toads differ, decidedly, from the results of Parker's (1903, p. 29) suggestive work on *Rana pipiens* Schreber. He found that these animals were positively phototropic in light, from a Nernst lamp, even at 20,480 ca.m. Without regard to the side of the frog that was exposed to the light, they turned and jumped toward its source. The frogs oriented themselves until they faced the source of illumination

and they remained in this position although the light was entirely unbearable to the human eye.

In connection with the responses of young toads both in and out of water, it would have been extremely interesting to have used a much longer experimentation trough in order to demonstrate whether or not the animals were seeking a certain optimum intensity of illumination. The writer planned to perform experiments of this nature if more material had been available at the time, and he hopes to do so in the future.

In connection with these responses of young toads to intense light, it is of interest to recall the work of Pearse (1910) relative to frogs and toads. This writer (*l.c.*, p. 175) found that *Rana clamata* moved toward a light of 225 ca.m. from a six-glower Nernst lamp. Five specimens were subjected to the light. He also states (*l.c.*, pp. 175–176) that *Rana sylvatica* was exposed to photic stimuli from a light of the same intensity. His results are summed up in the following quotation (*l.c.*):

> "This frog was more active than the last species, [*R. clamata*] and some individuals gave more decided phototropic reactions than did any member of the preceding species. There were, however, such differences in the reactions of the four animals used that they are tabulated separately. Individual No. 1 never failed to move straight toward the light. No. 2 was not as persistently positive after the eyes had been excised as before this operation, though it continued to give a majority of positive reactions. As individuals 3 and 4 were apparently indifferent to the light in their normal conditions, their eyes were not removed. The reactions of animals 1 and 2 were, however, strongly positive, and this condition remained even after the eyes had been excised; hence their skins served as photoreceptors as well as their eyes."

These results with frogs are quite different from the results of the writer with young toads. Such differences, however, are not at all surprising when it is recalled that not only are animals of different genera being considered, but also of different families; and further it must be kept in mind that on the one hand mature organisms are under observation and on the other very immature ones. Pearse (*l.c*,. p. 176) also experimented with *Bufo americanus* and *Bufo fowleri*. The records of the two species were not kept separate. The toads respond positively to a light of 225 ca.m., moving toward the source of illumination. Most of the animals used were adults, but a few were immature. None of them, however, were less than 2 cm. long. It has been demonstrated that the present writer finds young toads to respond negatively to the light from a projection lantern. The

difference in these results from those of Pearse is probably due to the fact that the writer employed more powerful stimuli in his experiments. Further, the writer used animals of much greater immaturity than was the case in Pearse's experiments.

III. RESPONSE TO LESS INTENSE ARTIFICIAL LIGHT

The young toads are next subjected to light of much lower intensity. The vessel containing the animals is placed directly in front of the bulb of an ordinary 16 c.p. incandescent electric light. Within the field of experimentation the illumination is approximately 44 ca.m. The first noticeable movement is the orienting response, all the toads so placing themselves, with respect to the light, that the longitudinal axes of their bodies become parallel with the longitudinal axis of the dish, which points directly toward the light. This response brings the toads into such a position that their heads are turned directly toward the source of illumination, and the median longitudinal axes of their bodies lie parallel with many of the rays passing through the bulb. However, with a light of this nature, it is incorrect to state, without qualification, that the median longitudinal axis of the body is parallel with the rays of light. Immediately after completing orientation, the toads jump in the direction of the light until they all reach the extremity of the vessel nearest to the source of illumination. The organisms remain oriented while traveling from one end of the glass trough to the other. Parker (*l.c.*) found that *Rana pipiens* Schreber oriented itself with its head toward the light and also moved toward the source of illumination. These were the responses to the intermediate light intensities between 1 and 20,480 ca.m. After the young toads had all reached the end of the vessel, it is turned around until the animals are moved to a position farthest from the source of light. They quickly perform the orienting response and again jump away toward the light. In this manner the animals are driven repeatedly from one end of the dish to the other. Usually, orientation is not performed so promptly nor do the toads jump so rapidly as in those experiments with the projection lantern. When the animals reach the end of the trough, they frequently climb up the end wall of the vessel as if to move still nearer to the source of illumination. There is no definite evidence that the median longitu-

dinal axes of the toads lie parallel with all the rays of light, for the rays emerge from the bulb at various angles and many of them must cross within the area of experimentation.

These results seem to indicate that young toads respond positively to incandescent light of 16 c.p. They orient themselves in such a manner that the long axis of the body lies parallel to some of the incoming rays and the head is turned directly toward the source of light. They retain this orientation with considerable precision while traversing the entire length of the experimentation dish. The fact that the animals move as near as possible to the light, and in some cases climb to the top of the glass wall at the end of the vessel, leads one to infer that the intensity of the light is a factor in causing the movements, rather than the direction of the rays *per se* in the field. In connection with the experiments on young toads just described, it is interesting to compare the work of Parker (*l.c.*) on *Rana pipiens* Schreber. He noticed the interesting fact that,

> "With the lower intensities the animals often did not react for from five to ten minutes or even longer, and the jumping response was frequently omitted; but their orientation was finally always with their heads toward the source of light, that is, positive. In some instances after a frog had remained ten minutes or more without changing its original position, it was induced to jump by being touched from behind, and, when this was done, the animal almost invariably turned first and then jumped toward the source of light."

It has been demonstrated that stimuli from a 16 c.p. incandescent electric light affects young toads in much the same manner as Parker has observed with reference to frogs. The toads orient more slowly to the weaker light than to the stimuli from the projection lantern. Movement toward the incandescent light is also more deliberate than toward the light from the projection lantern.

Dickerson (1906, p. 66) also has noticed that toads respond positively to artificial light of relatively low intensity. Her statement is as follows:

> "If we go to a pond at night, we shall have every opportunity both to see and hear toads, especially if we carry a lantern. Instead of being frightened by the light, they are attracted by it and may gather about it. If the lantern is set on the ground, they sometimes try to climb to its top."

The results of my experiments with less intense artificial light agree very largely with those of Cole (1907, p. 392) on *Acris gryllus* Le Conte. This observer states that the source of the

photic stimuli was an electric light situated 50 cm. above a flat surface on which the frogs were placed. *A. gryllus* faces the source of illumination and leaps toward it. When a frog jumps past the light, the animal remains with its back turned toward it for a short time. Then it turns in such a manner as to face the light and again leaps toward it. Cole (*l.c.*, pp. 393–401) also found that both *A. gryllus* and *Rana clamata* Daudin respond positively to light with an intensity of from 1.25–5 ca.m. by turning toward the source of illumination, but that individuals of the latter species were much the slower in their responses. He noticed that the positive response of *A. gryllus* occurs more quickly and uniformly when light of 5–20 ca.m. is used. This is in accord with the present writer's experiments on *Bufo americanus* as it is also in accord with the results of Parker (l.c.) with *Rana pipiens* Schreber already mentioned. It should be stated that during these experiments of Cole with *A. gryllus* and *R. clamata*, the animals were confined in glass boxes which were of such dimensions that the amphibians could turn readily in any direction, but were unable to jump away. My experiments are also essentially in agreement with those of Mast (1911, p. 219–220). This worker subjected seven toads to light from a single source. Two intensities were used, one of 12.5 ca.m. and the other of 25 ca.m. Five of these toads were small ones, but the exact size is not given. The following quotation presents the results which have more direct bearing upon the experiments described in the present paper:

> "They all oriented directly and fairly accurately. If placed on the table in the beam of light so that one side faced the glower they turned slowly but directly until they faced the light and then hopped or walked toward its source, stopping frequently for a few moments at intervals on the way. * * * The toads always went directly toward one or the other of the two sources."

IV. RESPONSE TO STRONG DIFFUSE DAYLIGHT

It was found that young individuals of *Bufo americanus* respond to diffuse daylight of relatively strong intensity, and a number of experiments were performed in which light of this nature was employed. The glass trough containing the toads was placed on a table, having a black surface, at a distance of 50 cm. from an east window. A glass plate, painted a dead black on the under side, was placed over the top of the experimentation dish. Then the strip of black paper, covering the

end of the vessel facing the light, was removed. Such an arrangement modified, considerably, the effects of the cross rays.

It is noticed, after the dish containing the toads has been near the window for a few seconds, that the animals orient themselves with their heads toward the source of light and with the long axes of their bodies parallel with the longitudinal axis of the vessel used for the reaction work, but not parallel with the great majority of the rays, for these enter the dish at various angles notwithstanding the precautions already described. The toads jump away in a comparatively straight line toward the light. All the organisms are soon congregated at the end of the trough nearest to the window. Not infrequently some of them climb up the glass wall at the end of the dish and cling in that position. The vessel is turned around until the end where the toads are gathered is pointing directly away from the window. Those that are clinging to the glass side drop down to the floor of the trough. All the animals again turn their heads toward the window and move off, with the long axes of their bodies parallel with the longitudinal axis of the experimentation dish, in the direction of the source of illumination. In a short time they are all found at the extremity of the vessel. Experiments of this nature are continued for eight successive trials. Each time the animals move promptly from one end of the dish to the other. As in the experiments with incandescent electric light, there is evidence that orientation does not occur quite so promptly nor is locomotion so rapid as in the experiments with the projection lantern.

These experiments appear to indicate that young toads respond positively to diffuse daylight of somewhat strong intensity. They also exhibit definite orientation with the anterior end of the body turned directly toward the light. But it cannot be said that the long axis of the body lies parallel to the incoming rays, for it is evident after careful consideration that these must enter the experimentation trough at many and varied angles, numbers of them passing, more or less, along its entire length.

The responses of toads and frogs to strong diffuse daylight have been observed by other workers, and a brief comparison will be made with the results of some of their experiments. It is of interest to notice that, Graber (1884, p. 124) found that toads, *Bufo vulgaris* Laur, placed in a box with two compart-

ments, one of which was darkened and the other exposed to diffuse daylight, moved toward the darkened compartment and tended to collect there. According to Graber's (*l.c.*, pp. 39, 40) description of his own methods used in experimentation, the natural inference is that he used strong diffused daylight as a source of stimulation, except in those instances where it is stated specifically otherwise. The following quotation presents his results (*l.c.*):

"Da die meisten Versuche, die ich mit diesen ekelhaften Tieren anfieng, ein negatives Resultat ergaben, glaubte ich mich in eine genauere Lichtgefühl-Prüfung nicht einlassen zu sollen und geh' ich auch bei der Mitteilung der erhaltenen Reactionswerte ganz summarisch zu Werke.

"Aus der Vergleichung von Weiss und Schwarz geht zunächst hervor, dass, wie zu erwarten war, die dunkle Abteilung der hellen bei weitem vorgezogen wird.

$$\text{"1)} \quad \frac{\text{Weiss}}{\text{Schwarz}} = \frac{1}{8.4}.$$

"Darnach ist also die Lichtscheu der Kröte (obiger Quotient beruht freilich nur auf 5 aber unter sich übereinstimmenden Beobachtungen) entschieden viel grösser wie jene des Frosches (aber kleiner wie die des Triton)."

While it is evident that the results of Graber's experiments differ from those of the writer, yet attention should be drawn to the fact, as indicated in the first paragraph quoted, that there was evidently some doubt in the author's mind as to the correctness of his own results. Plateau (1889, p. 82), however, working with *Rana temporaria* and *Bufo calamata* reached conclusions of an opposite nature. He demonstrated, when specimens were liberated in an experimentation box lighted by windows at one end only, that both specimens responded positively to the light and jumped toward the source of illumination. One infers from Plateau's (*l.c.*, p. 81) statement that strong diffuse daylight was used in his experimental work with amphibians. According to Loeb (1890, p. 90) frogs respond negatively to strong diffuse daylight. Torelle (1903, p. 469) experimented with *Rana virescens virescens* and *Rana clamata* and demonstrated that both species oriented in such a manner that their heads pointed toward the source of illumination, diffuse daylight, and also that they moved toward the light. Dickerson (*l.c.*, p. 32) states that the frog moves toward diffused light, probably meaning strong diffuse daylight.

V. RESPONSE TO WEAK DIFFUSE DAYLIGHT

A number of experiments were performed with weak diffuse daylight. The light was obtained from a south window. The incoming rays passed through a small slit-like opening in the wall of the dark room before reaching the experimentation dish. The length of the opening corresponded with the width of the vessel and the width of the former was equal to the depth of the latter. The window through which the light entered was 4 m. distant from the dark room (see Fig. 1, A).

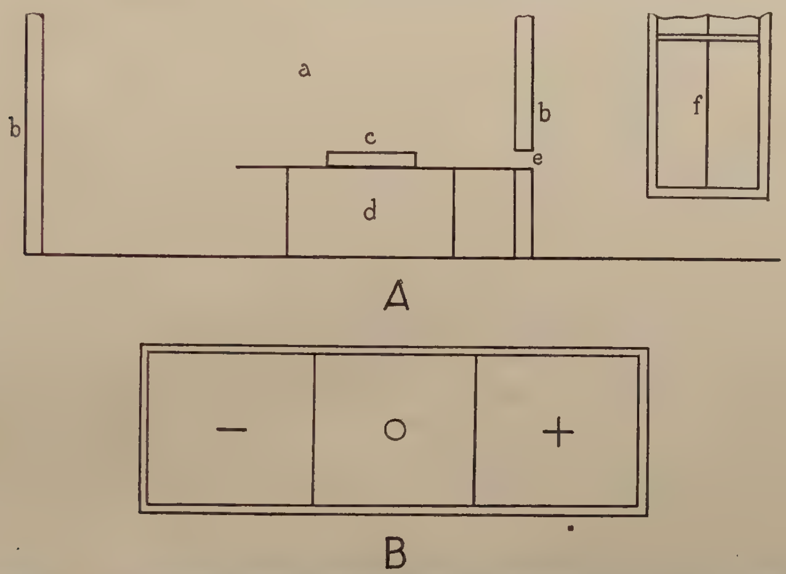

FIGURE 1. A. Sectional diagram showing plan of apparatus employed in testing responses of young toads to stimulation from weak diffuse daylight. B. Experimentation dish enlarged more than is shown in A. a, Interior of dark room; b, walls of dark room; c, experimentation dish containing young toads; d. table; e, opening through which light enters dark room; f, window through which light enters, situated in wall of outer room; +, positive; —, negative; 0, indifferent. (Not drawn to scale.)

The glass trough containing the toads was placed in close proximity to the slit-like opening. It was noticed that there was no immediate response to the light, neither by orientation nor by movement toward or away from the source of illumination. This being the case observations were taken every fifteen minutes, and the positions of the animals in the dish noted. The

vessel was divided by transverse lines into three equal divisions (see Fig. 1, B). Toads found in the section marked + were considered to respond positively to the light. Those gathered in the division marked — were enumerated as responding negatively. The organisms congregated in the space marked o were counted as being indifferent to the illumination. Table I indicates the results of six experiments with twelve individuals used in each experiment.

TABLE I

Responses of Young Toads to Weak Diffuse Daylight

Number of Experiments	Positive	Indifferent	Negative
1	7	2	3
2	6	1	5
3	8	2	2
4	6	2	4
5	7	1	4
6	8	2	2
Totals	42	10	20

The above table shows that out of a total of 72 responses, 42 of them may be considered as being positive, 20 as being negative, and 10 as being indifferent. The writer performed many other experiments beside those indicated in Table I, some of which showed a rather higher percentage of positive responses than evidenced in the table; but it is believed that the results indicated there present a fairly representative series. From these results the inference is drawn that young toads respond positively to weak diffuse daylight. However, the orientation of the animals lacks the definiteness exhibited in the experiments with light of stronger intensities. Neither the motor response nor the orientation is so precise as is the case in the experiments with strong diffuse light. Many of the toads that collected in the section marked + faced the slit-like opening in the wall of the dark room through which the light entered. Those toads that faced the light have the median longitudinal axes of their bodies parallel with the longitudinal axis of the experimentation dish and also parallel with a portion of the incoming light rays. But it must be remembered that the rays cross at many and varied angles, and while it is true that

many of these cross lights are cut out as the rays enter the dark room, yet it would be incorrect to state that all the rays of light are parallel with each other and with the median longitudinal axis of the bodies of the toads facing the light.

Graber (*l.c.*, pp. 120, 121) while making observations on *Rana esculenta L.*, stimulated by means of weak diffuse daylight, "meist trüber Himmel," states results which lead to the inference that these animals react negatively to photic stimuli of such a nature. However, their responses were not so preponderantly negative as was the case of *Bufo vulgaris* Laur already mentioned. The following quotation will give an idea of his results (*l.c.*, p. 121):

"Auch zeigt der Versuch, dass das Reactions-Verhältnis ein sehr constantes ist, indem die Weiss-Frequenz sich zwischen 11 und 18 und die des Schwarz zwischen 22 und 29 bewegt, und grössere Extreme, wie solche sonst sehr häufig sind, mit Ausnahme eines einzigen Falles (7:33) gar nicht vorkamen.

"Das Mittel-Verhältnis ist:

$$1)\ \frac{\text{Weiss}}{\text{Schwarz}} = \frac{1}{1.5}."$$

Loeb (*l.c.*, p. 89) experimented with frogs subjected to weak diffuse daylight, and found that they responded by moving away from the light.

VI. RESPONSE TO SUNLIGHT

No systematic experiments were undertaken in order to determine the effect of sunlight on the behavior of young toads. However, a few incidental observations were made and these were recorded.

The young toads were kept in a large glass aquarium jar when not under experimental observation. This chanced to be placed near a window with an eastern exposure. A narrow beam of sunlight entered the dish, and to one side of these rays of bright light was diffuse daylight. The animals jumped toward the side of the jar at which the sunlight entered. Usually they remained in the sunlight for some time. This response seemed to vary, for certain individuals remained in the direct light longer than others. However this may be, there was certainly a response to sunlight, evidenced by the toads jumping toward the window where the sunlight entered. Frequently the animals were found in the less illuminated portions of the jar,

but they usually remained at the side of the vessel nearest to the window. On sunny days the writer often has observed that young toads respond both to moving shadows and moving objects. Sometimes they respond by crouching against the ground, and at other times by the jumping response. The response to moving objects has been noticed also on cloudy days. The writer did not employ a heat screen during any of these observations. Therefore there was no definite attempt to isolate possible temperature responses from photic responses. However, he infers from the experiments of Pearse (*l.c.*, pp. 192–195) that these responses are probably not due to temperature. My observations were recorded in the middle of the day, during the month of July. Similar responses occurring in the early spring or late fall may be due largely to temperature.

Torelle (1903, p. 469) working with *Rana virescens virescens* and *Rana clamata* noticed, in one series of experiments, that specimens of both species responded positively to sunlight, but that they did not stay in the circle of most intense illumination. Some individuals moved away without turning. Others turned and retreated some distance, and then oriented themselves with their heads pointing toward the incoming beam of sunlight. In another series of experiments in which specimens of the same species of frogs were placed in a box, admitting sunlight at one end and diffuse light at the other, Torelle (*l.c.*, p. 471) found that the animals "turned toward and moved to the end" where the sunlight entered. They did not stay within the area of strongest light, for they either moved to the opposite end of the box, or else backed, without turning, into the region where the light was less intense. These results correspond more or less to my observations on young toads; although unfortunately the present writer did not observe the kind of response when the animals moved into the less illuminated area. Dickerson (*l.c.*, p. 71) has noticed the response of young toads to sunlight. She states that, "They congregate in large numbers on sunny brown earth patches." Such places are near or among the grass. The observations of Miller (1909, pp. 659–660) are in accord with those of Dickerson. The former has noticed that toads are rarely seen during the day unless it is cloudy. Late in the fall, however, they are found in the sunlight, among the grass. It should be stated that none of these

writers, Torelle, Dickerson and Miller, indicate clearly whether the response is due to light or temperature.

VII. RESPONSE TO COLORED LIGHT

A few experiments of a very general nature were performed with colored light as the source of stimulation. The young toads were subjected to the stimuli from a 16 c.p. incandescent light. At first the light was passed through glass of various colors. Later the rays were transmitted through colored solutions prepared according to the directions recommended by Nagel (1898, pp. 649–655). Such light proved to be more nearly monochromatic, as was seen on examination with the spectroscope. The solutions were placed in a glass cell with parallel sides. Red and blue are the only colors that will be referred to here.

The young toads are seen to be scattered promiscuously throughout the experimentation dish when it is placed in the beam of light transmitted through the red solution. Frequently there is observed to be considerable hesitancy before the animals orient themselves with reference to the light. Some of them turn toward the light, while others exhibit no definite orientation. In some experiments it is observed that the number of toads responding positively to the light is slightly in excess of those responding negatively; but in other experiments the reverse proves to be the case, for the number of animals exhibiting the negative response to the light is somewhat greater than those exhibiting the positive response. Usually, however, it may be stated that a small majority of the toads turn in such a manner that their heads point toward the source of illumination. Some animals orient a few seconds after they are placed in the beam of light. Others wait much longer than this before they turn either away from or toward the red light. Certain individuals jump in the direction in which their heads are pointing, immediately after orientation is completed, while others wait from a few seconds to several minutes before they jump away. The jumping movement toward the red light is far less common than is the case with reference to the blue light. In general it may be said that the movements of young toads away from and toward the source of illumination are slower and with more and longer pauses between the jumps than is the case when

white light is used. It is evident that red light is not a very effective form of stimulus, certainly the toads are not nearly so responsive to it as they are to white light.

In the experiments with blue light the toads are observed to be distributed at various different points in the experimentation dish. This is placed in the beam of light emerging from the blue solution. The animals turn with promptness toward the source of illumination. In most cases they jump immediately toward the light, or with a delay of but a few seconds. There are comparatively few pauses between the jumps and these are of short duration. Not only is the orienting response more prompt, but the movement toward the light is also more vigorous than is the case when the red solution is used. The orientation of the toads and their movement toward the source of illumination are very similar to the results observed with the 16 c.p. incandescent light when neither the red nor the blue solution is used.

Torelle (*l.c.*, p. 478) found when single colored lights were used that specimens of *Rana virescens virescens* and *Rana clamata* always jumped in the direction of the blue light and remained with their heads pointed toward it, touching the glass. On a frog being placed close to the red light, it usually turned away from the source of illumination. In some cases the animal not only turned, but jumped away from the red light. When a frog was placed about 30 cm. away from the red light, the animal generally remained there and did not jump toward the light. According to the experiments of Pearse (*l.c.*, p. 189) with *Rana palustris*,

> "The results show that the blue is apparently the most effective in the production of positively phototropic reactions, and that there is a regular graduation from blue to red, both in the percentage of positive reactions and in the rapidity with which the movements took place. * * * It is probable that these differences in the reactions are due to differences of the wave lengths, but they may be due to intensity differences."

These results of Pearse with *R. palustris* are largely in accord with those of the writer with young toads. Results similar to those of the writer on young toads when blue and red lights were used were obtained by Laurens (1911, p. 267). He subjected *Bufo americanus* and *Bufo fowleri* to the stimuli from single monochromatic lights of equal intensity, using Nernst

glowers for the source of illumination, and showed that members of both species reacted by giving motor responses, turning and jumping toward or away from the light. In one series of experiments with blue light, there were 251 positive responses and 37 negative ones. In another series of experiments with red light, there were 167 positive responses and 121 negative ones. The former series shows the percentage of responses to be 87 positive to 13 negative, while the latter series shows the percentage of responses to be 58 positive to 42 negative.

> "By way of summarizing the results of the experiments with single monochromatic lights in which both the eye and the skin acted as receptors, it may be stated that all four colored lights used produced positive responses. Blue light was the most effective, and the other lights formed a decreasing series, corresponding roughly to their relative position in the spectrum, the red light being but slightly more effective than darkness." (Laurens, *l.c.*)

This summary presents results which are in extremely close agreement with those of Pearse (*l.c.*) on *Rana palustris.*

Some observations were recorded when stimuli from light of different colors, red and blue, were impinging upon the toads at the same time. The glass vessel containing the animals was so placed that the red light was situated at one extremity and the blue light at the other. The position was such that one end of the dish was in the beam of red light and the opposite end in the beam of blue light.

The young toads are placed in the center of the dish, approximately half way between the lights passing through the red and blue solutions. There is little more exhibited in the resulting responses than has already been recorded with reference to the single colored light. Orientation and movement toward the blue light are more definite and more vigorous, than they are with respect to the red light. By far the majority of the animals jump toward the blue light. A few individuals jump toward the red light. These make longer pauses between the jumps than is the case of those toads moving toward the blue light. Frequently periods three minutes or more in duration elapse between some of the jumps. At times one or two specimens appear to be indifferent to either light. In several instances observations were recorded after a period of fifteen minutes from the time the toads were first placed in the experimentation dish. In these experiments twelve toads are used each

time. Table II indicates the position of the toads with respect to the two colored lights for four sets of observations.

TABLE II

Responses of Young Toads to Colored Lights

Experiment	Blue	Red	Indifferent
1	10	2	0
2	7	3	2
3	10	1	1
4	9	2	1
Total No. of Responses	36	8	4

It is seen from the table that out of a total of 48 responses, 36 are toward the blue light, 8 are toward the red light, and 4 are indifferent, apparently being no response to either of the colored lights. The blue is evidently by far the more effective color with respect to the responses of young toads when stimuli from both red and blue light are impinging upon them.

The results recorded above are largely in accord with those of Graber (*l.c.*, p. 125) on *Bufo vulgaris* Laur as indicated in the following quotation (*l.c.*):

> "Dass auch bei diesen Reactionen wieder in erster Linie die Helligkeitsverhältnisse ausschlaggebend sind, geht schon aus dem Umstande hervor, dass einerseits Dunkel-Rot, andererseits Dunkel-Blau vorgezogen wird. Speciell aus der ersten Vergleichung, wo Rot sehr bedeutend dunkler als Blau und doch nur wenig stärker als letzteres besucht ist, könnte aber vielleicht geschlossen werden, dass diese Farbe als soloche der Kröte weniger angenehm als Blau sei. * * *
>
> $$2)\ \frac{\text{Rot}}{\text{Blau m. uv.}} = \frac{1}{1.2}\ ?\text{''}$$

While it is true that in one series of experiments when "Dunkel-Rot" and "Hell-Blau" lights were employed, the number of responses were 305 toward the former and 288 toward the latter, or in proportion of 1 : 0.9, yet in another series when "Hell-Rot" and "Dunkel-Blau" were used, the responses were 108 to 142, or in the reaction-proportion of 1 : 1.3. Graber (*l.c.*, p. 122) experimenting with *Rana esculenta* L. obtained results somewhat at variance with those of the writer on young toads. The lights employed were "Hell-Rot" and "Dunkel-Blau." Three sets of experiments were performed, each con-

sisting of ten trials. There were 736 responses toward the red and 464 toward the blue. The following quotation gives a brief statement regarding the experiments (l.c.):

> "Da Rot, trotzdem es heller als Blau war, in 30 Fällen 26mal stärker als letzteres besucht wurde, unterliegt es wol keinem Zweifel, dass dasselbe dem Frosch, ähnlich wie dem Triton, viel angenehmer als das Blau ist. * * *
>
> "Als (Minimal)-Verhältnis ergibt sich
>
> $$2)\ \frac{\text{Rot}}{\text{Blau m. ult.}} = \frac{1}{0.6}.$$
>
> d. h. es kommen auf 10 Rot- durchschnittlich nur 6 Blau-Besuche."

The results of Graber's experiments with *Rana esculenta* L., according to Torelle (*l.c.*, p. 487),

> "Can be explained only on the ground of a confusion arising as a result of using so many frogs (forty) at the same time in one receptacle."

As will be shown, Torelle (*l.c.*, pp. 478, 479) obtained results with frogs, *Rana virescens virescens* and *Rana clamata*, exposed to the stimuli of red and blue lights both at the same time, much at variance with those of Graber (*l.c.*). For experimental purposes Torelle used a low, narrow box about 45 cm. in length with a glass plate at each end. Red light was admitted at one end of the box and blue at the other. The frog was then submitted to the influence of the two lights. The response toward the blue light was immediate, the animal moving toward the source of illumination. Frequently the frog remained with its head against the glass and turned toward the light. Apparently there was no movement on the part of the frogs toward the red light. These results of Torelle's with frogs are largely in agreement with those of the writer with specimens of young *Bufo americanus*, as they are also with the statements of Holmes in regard to frogs. According to this author (1907, p. 349) the blue and the violet rays are the most effective in producing phototactic responses. When two lights are used, red and blue, frogs collect near the blue light.

The results of the writer with specimens of young *Bufo americanus* and those of Laurens (*l.c.*, pp. 277–282) with *Bufo americanus* and *Bufo fowleri* are in accord. He worked with pairs of balanced colored lights and found that the toads reacted by giving motor responses, either jumping toward or away from the source of illumination. The animals also responded by

orienting themselves so that their heads pointed toward or away from the light. In one series of experiments with red and blue lights, out of a total of 960 responses, 788 were toward the blue light, 167 were toward the red light, and 5 were indifferent. Viewing the responses from the percentage basis, 82 per cent were in favor of the blue light, while only 17 per cent were in favor of the red light. It will be noticed that the results in the main are similar to those obtained with single monochromatic lights. However, it should be stated that the responses were not quite so quick as was the case with single lights. There were movements toward both lights, but those toward the blue far outnumbered those toward the red.

> "It cannot be said that there is much evidence in favor of positive phototropism for the red light." (Laurens, *l.c.*, p. 280.)

In comparing these experiments of Laurens, with balanced blue and red lights, with those of Pearse (*l.c.*) on *Rana palustris* with single blue and red lights, it is of interest to observe that the results in the two cases very largely agree, in that there is a greater number of positive responses toward the blue light than there is toward the red light. However, it should be noticed that there is a much larger percentage of positive responses with reference to the blue light in the former's experiments with balanced blue and red lights, than is found to be the case in Pearse's experiments with blue and red lights used singly. It should also be noticed that in Pearse's experiments the results indicate many responses that were indifferent with respect to the red light.

VIII. RESPONSE TO CONTACT

Some observations were made on young specimens of *Bufo americanus* with reference to their responses to contact stimuli. While no systematic experiments were undertaken in order to study the effect of contact on the behavior of the animals, yet certain incidental observations were recorded. Some data were obtained regarding the influence of contact stimuli on the response to light. Record was made of observations on a form of a contact response resembling the death-feint among Arthropods. Some description also was given of the work of other writers with regard to the contact responses of toads and frogs.

During the experiments with light there were usually a num-

ber of young toads in the experimentation dish at the same time. Occasionally in jumping toward or away from the source of illumination two individuals come in contact with each other. Frequently this contact appears to have no effect upon the animals so far as their response to light is concerned. At other times one or both of the toads pause for a few seconds before again reacting with the motor response with reference to the light. Generally, however, when contact occurs it seems to act as a stimulus in inducing the motor response. This is noticeable when a toad, in jumping, comes in contact with a stationary individual, the latter's motor response being invoked. If a toad does not respond to the light for a few seconds, but remains quietly resting in one position, and if then it is stimulated by means of another animal jumping against it, the motor response may result and this may be followed by the animal responding to the photic stimuli. These statements apply more largely to the experiments with the weaker intensities. Parker (*l.c.*, pp. 28, 29) found when subjecting frogs, *Rana pipiens* Schreber, to the lower light intensities from a Nernst glower that,

> "In some instances after a frog had remained ten minutes or more without changing its original position, it was induced to jump by being touched from behind, and, when this was done, the animal almost invariably turned first and then jumped toward the source of light."

Pearse (*l.c.*, pp. 177, 178) in discussing "the influence of mechanical stimulation on the photic reactions of the toad," *Bufo americanus* and *Bufo fowleri*, when subjected to a light intensity of 220 ca.m. states that,

> "In jumping about they stimulated each other in a mechanical way. * * * It is evident * * * that mechanical stimulation exerts an influence on the phototropism of the toad by enforcing the effect of light, or, it could perhaps better be said, that the mechanical stimulation furnishes the *impulse* to locomotion, while the light is effective in *determining* the direction of the movement after locomotion has been established."

The writer has noticed in his experiments with the less intense illuminations that when several young toads move into the angles formed by the bottom and sides of the experimentation dish that the contact of their bodies and of the solid surfaces of the vessel seem to inhibit the motor response for some time. The animals remain quietly resting with their bodies in rather close contact. During the experiments with weak diffuse daylight, it was found that when stones were placed about 25 mm. apart

in the experimentation dish that there was a tendency for some of the toads to move into the spaces between the stones. The writer has frequently observed a similar "habit" on the part of mature and partially mature frogs. Large numbers of frogs, chiefly *Rana pipiens* Schreber, were kept in two large tanks in a basement room, the tanks being in diffuse daylight. It was a very common sight to find as many as thirty individuals crowded closely together in the angles formed by the sides and bottom of each tank. Frequently they were congregated in the more shaded corners, and the taking of such positions might be due in part to a response to light. However, they were sometimes observed to be gathered in corners that were not so shaded. At other times frogs were found to be grouped in the corners of the tanks, both in shaded and unshaded situations. Not infrequently frogs were observed to be distributed sparsely about the more central and open portions of the tanks. Such groupings as have been described are in all probability due to responses to contact stimuli. The movement into the shade may be due in part to vision as Torelle (*l.c.*, p. 470) has suggested.

Other writers have recorded observations on the contact responses of toads and frogs. Torelle (*l.c.*, p. 477) experimented with specimens of *Rana virescens virescens* and *Rana clamata* in a jar of water and found that the propensity of the frogs to place themselves in contact with solid bodies "is apparently stronger when the temperature is lowered." The following interesting facts are quoted from the author's work cited above:

> "When a rock was lowered into the jar in such a way that a small space was formed between it and the wall of the jar, the frog crawled into this space and remained there. When a space was formed between the bottom of the jar and the rock, it crawled into that. This was tested several times, and was also observed when the temperature of the water in the aquarium in which the frogs were kept was lowered 10° C. and below. When this was done, all the frogs responded, either by flattening their bodies against the stone floor, or by creeping under the rocks usually kept there. It therefore seems that the frog is stereotropic in temperatures between 10° C. and 4° C."

These experiments of Torelle's, considered with those (*l.c.*, p. 476) on frogs out of water, seem to bear an interesting relation to hibernation. It is probably true that this instinct is not due to a single but to several causes. The increase of stereotropism with a lowering of the temperature is an important physiological change which may be related to the burrowing

response of hibernating frogs. Dickerson (*l.c.*, p. 71) has observed the tendency of young toads, *Bufo americanus* Le Conte, to crawl "under stones and chips, in the cracks of board-walks or under the protecting cover of leaves and grasses." The young toads to which she referred had left the water just recently and were therefore very delicate creatures, and they remained during the daytime in such protected situations as have been mentioned. So that while these responses are probably due in part to contact stimuli, yet other stimuli also such as light and temperature undoubtedly have considerable influence in bringing them about. The burrowing response of young spadefoot toads, *Scaphiopus holbrookii* Harlan, exhibits itself early in the life of the individual (Dickerson, *l.c.*, p. 56), and is in part at least a response to contact. According to Holmes (*l.c.*, p. 351) there is a tendency for frogs and toads to crawl under stones and to place themselves between objects. In such positions they remain quiet. This propensity to move into such situations is more pronounced in the case of toads. He considers such responses to be of a thigmotactic nature, although from his discussion it may be inferred that at times light also plays some rôle.

Considerable care was used in handling the young toads during the experiments with light. They were removed from the aquarium jar and placed in the experimentation trough by hand. In order that such contact should modify the response to light as little as possible, the toads were left undisturbed for approximately fifteen minutes before being subjected to the photic stimuli of the experiment. Should the toads while being transferred from one vessel to another be handled with undue pressure and roughness, they sometimes assume an immobile state. As this response was a somewhat unfamiliar one to the writer a number of observations were recorded concerning it.

Frequently when young specimens of *Bufo americanus* are handled, the contact stimulus causes them to become motionless; they react with the death-feigning response. Certainly they assume an attitude which is comparable to that assumed by many Arthropods when they are said to feign death. The legs are drawn up closely against the body and they assume a more or less rigid condition, the animal remaining motionless. Sometimes a toad lies so absolutely quiet that even the respiratory

movements are unobserved, and the eyes may be closed. The attitude assumed by the death-feigning animal is not always as just described. Instead of the legs being drawn up in close contact with the body they may be somewhat extended. A young toad may be made to feign death by being placed on its back in the hand or on the laboratory table, and held in that position for a few seconds. There is considerable variation among different individuals regarding the length of time of the death-feigning response. Some feign death for a few seconds only, while others retain the death-feigning posture for a minute, and occasionally even for a longer time. When young toads are exposed to the beam of light from the projection lantern during the death-feint, the length of the response seems to be somewhat shorter, than when the animals are induced to feign death in weak diffuse daylight. Here again there is much variation, for in some instances it appears to make no difference to the toad as to the intensity of the light to which it is subjected. If the animal is put into the death feint in diffuse daylight and is then exposed to the bright beam of light from the projection lantern, the length of the response is curtailed, in fact the toad at times arouses immediately from the death-feint. A young toad generally arouses from the death-feint rather suddenly. If the animal is on its back, first one leg and then another is extended until the legs are no longer pressed closely against the body. If the eyes are closed while in the death-feint, they are opened sometime during the process of arousing from the response, while the legs are being extended. Immediately after the eyes have been opened and the legs extended, the toad turns over with the ventral side down. While it is true that the young toad usually arouses from the death-feint rather abruptly, there are individual variations, some animals being more deliberate in the process than is the case with others. Young toads may be promptly aroused from the death-feint by sudden tactual stimuli, as for example, a touch on the body, though this may at times cause a continuance of the response, or by dropping them into a jar of water. Dickerson (*l.c.*, pp. 71–72) has observed the death-feigning response in young toads, as indicated by the following quotation:

> "When they are handled they play dead for seconds at a time and finally 'come to life' sticking up their little orange paws in most ridiculous fashion before they tumble over and hop away."

Mature specimens of *Bufo americanus* will also feign death. The writer has frequently caused toads to exhibit this response by placing them with the back down and in close contact with some solid surface, meanwhile holding them firmly in that position for approximately thirty seconds more or less. They sometimes respond to stimuli of this nature by feigning death for one or more minutes. Near Ann Arbor, Michigan, the leopard frog, *Rana pipiens* Schreber, is very common. Mature specimens taken in that locality frequently have been made to exhibit the death-feigning response by rough handling and by placing them on their backs on the laboratory table and holding them securely for some time in such a position. Mature toads and frogs exhibit much individual variation in reacting with the death-feigning response. The response is elicited in some animals much more readily than in others. In some instances it seems to be practically impossible to induce the response. The length of the death-feint also varies considerably in different individuals. The death-feigning response is undoubtedly of the same nature as that which Verworn (1898) [3] calls hypnosis. According to this writer specimens of *Rana esculenta* when turned on their backs, become motionless. Sometimes the hind legs are drawn close to the body, and the eyes are closed. While the animals lie in this position, their muscles are in a condition of "tonic contraction." Hypnotized frogs may assume peculiar attitudes, as if in attempting to right themselves the movements were suddenly inhibited. Verworn (1899, pp. 358–359) in discussing the hypnotic state of frogs makes the following statement:

> "The phenomena of prolonged reflex tone after brief stimulation may be seen still more clearly in frogs that have been deprived of their cerebrum. If such a frog sitting quietly in the customary squatting attitude be gently stroked by two fingers along the sides of the spinal column, he raises himself upon his extremities by contracting their muscles, and stands, sometimes more than an hour, in this grotesque position."

According to Verworn (*l.c.*, p. 496) if a frog is seized suddenly and held with a firm grip, and is then placed with its back down the animal remains immobile. A very peculiar contact response on the part of certain toads, *Bombinator igneus* and *Bombinator*

[3] Beiträge zur Physiologie des Centralnervensystems I. Die sogenannte Hypnose der Thieren. Jena, 1898, pp. iv+92. This paper was not accessible, but some discussion of it is given in the section on "Hypnotism," Holmes (1907, pp. 59, 60, 61), and in a review by Gotch (1898).

pachypus, appears to be somewhat akin to the death-feint, or to the hypnotic state already described. The following quotation taken from Gadow (1901, p. 156) gives a good description of the posture assumed by these toads during the response:

> "When these toads are surprised on land, or roughly touched, they assume a most peculiar attitude. * * * The head is partly thrown back, the limbs are turned upwards with their under surfaces outwards, and the whole body is curved up. * * * The creature remains in this strained position until all danger seems passed."

The following interesting description of the death-feigning instinct among toads and frogs is given by Dickerson (*l.c.*, p. 34):

> "Many of the Salientia play dead in response to an unexpected tactual stimulus. The common toad will often hold the legs tight against the body and inhibit all movement—even the breathing vibrations of the throat—when seized by a dog or other enemy. The leopard frog may stretch the legs backwards stiff and straight, fold the arms on the breast, and inhibit the breathing movements. It certainly looks like a dead frog as it lies motionless in one's hand for fully a minute; suddenly, with a lightning movement, it is gone before the hand can be closed over it. The cricket frog plays dead in water. Taking a position with arms and legs rigid and throat collapsed, it floats about helplessly like any stick or leaf."

Dickerson (*l.c.*, 87–88) considers the death-feigning response of the toad to be a protection to the animal. She states that,

> "The toad is fitted for his place in life by what he does, as well as by what he is. Let an enemy seize him roughly, and he is a dead toad. 'Playing dead' saves him many a time. He will lie on his back with scarcely any perceptible motion for minutes at a time. Even the breathing movements seem to be suspended. Suddenly one leg is thrust out, then another, the eyes open wide, and in an instant more, the toad has turned over and is ready for new emergencies. Whether this habit is a protective instinct, or whether the toad really is insensible from fright during the time that it 'plays dead,' the resulting protection is the same, for, as a rule, animals that feed upon living food associate motion with life so firmly that they pay no attention to a motionless creature."

Facts similar to those described by Dickerson have been observed by Holmes (*l.c.*, pp. 59, 60, 61), who considers this immobile condition of the frog to be an hypnotic state. According to this author the position assumed varies at different times. Some individuals are more easily hypnotized than others, and the duration of the hypnotic state also varies in different frogs. Sometimes a frog will remain immobile for hours. A frog may be aroused from its condition of hypnosis by some sudden stimulus, and the awakening often occurs immediately.

Sometimes when removing the young toads from the aquarium jar to the experimentation dish, the writer observed that the

animals respond to contact in another manner than that of the death-feint. The body of the toad is spread out and closely pressed against the bottom of the aquarium, and the lungs are filled with air until the animal becomes as wide as it is long. The head is also bent downward and placed on the bottom of the aquarium. As long as the animal retains this position it remains motionless. Reactions similar to these may occur as responses to a moving shadow or object, as for example the writer's hand when it is reached into the aquarium to remove the young toads. So that these are responses to both tactual and visual stimuli. Dickerson (*l.c.*, pp. 33–34, 86) also has drawn attention to this form of response in the toad. According to Holmes (*l.c.*, p. 32),

> "Frogs sometimes swell the body before being seized as if in anticipation of their capture, and they are especially apt to do this after being lightly touched. Touch a frog that is resting quietly, and if the creature does not hop away, one may see the body puff up; and if the body is touched two or three times, the swelling will continue until the lungs contain their maximum amount of air. * * * Frogs often avoid capture better by remaining perfectly quiet than by attempting to get away by jumping. * * * Safety is also sought occasionally by crouching close to the ground, and more often by crawling under some object that promises to afford shelter."

Another interesting response to contact stimuli is the "singing" or croaking of frogs and toads. The croaking of frogs and toads is readily induced by stroking the body, especially on the back or sides. They also will croak when kept in an aquarium. The contact of one animal against another is often sufficient stimulus to produce this sound. It is not improbable that light as well as contact may play some rôle in connection with the croaking reflex. The writer frequently has observed hundreds of toads in bright patches of moonlight along the shores of ponds and marshes. On such occasions their heads are raised, and the throat-sac is puffed out to a large size, owing to their vigorous "singing." At such times they give little "attention" to the observer, and one may pick up a toad, placing it upon the palm of the hand where it will continue to "sing" with astonishing vigor.

IX. DISCUSSION

It has been pointed out, in the experiments with the projection lantern, that young specimens of *Bufo americanus* orient in such a manner with reference to the light that the head points

away from the source of illumination. After orientation is completed the animals retain the position assumed with reference to the light, the medium longitudinal axis of the body being kept practically parallel with the incoming rays. So far as the writer's observations are concerned, there is no definite evidence that young toads orient to light according to the method of "selection of random movements," as advocated by Holmes (1905) (though the present writer believes that it may function in some modified form), or by that of "trial" so ably propounded by Jennings (1904) and (1906), also discussed by Mast (*l.c.*,), and many other writers. Usually the young toads orient promptly and definitely. If the head is pointing toward the light, they make a turn of 180° so that the anterior end of the body is pointed directly away from the source of illumination. Should the toad be in such a position that the median longitudinal axis of the body lies at right angles to the rays and facing the light, the animal makes a turn of 90°, thus bringing the head into such a position that it points directly away from the source of illumination. There are no preliminary movements, either "trial" or "random" ones, during or immediately preceding the orienting response, so far as the writer observed. But as Mast (*l.c.*, p. 214) has suggested, these facts do not preclude the possibility of preliminary movements when other forms of stimuli impinge upon the toads. After orientation is completed the young toads jump away from the source of illumination along a comparatively straight path, the medium longitudinal axis of the body being parallel with the rays of light. During such motor responses the direction of the rays in the field may be a guiding factor. It is not impossible that they may be both a guiding and a correcting factor, if we should apply the theory advocated by Holmes (*l.c.*, pp. 108–109). While there is little evidence of such responses on the part of young toads, nevertheless the applicability of Holmes's modified "trial and error method" with reference to the responses of animals which orient themselves "according to the usual scheme" is worthy of careful consideration. The present writer believes that it is absolutely futile to attempt to explain the responses of all animals by any one theory, or from any one point of view.

Such a response on the part of young toads as has been described by the writer is a tropic response in so far as it fits

the definition of Jennings (1909, p. 307), however, the writer does not wish to be understood as believing that internal factors, changes in bodily states, play no rôle in the orientation of young toads to light. This matter was not discussed in connection with the responses to intense artificial light, largely because the wr ter was attempting to record the responses as they occurred in the majority of cases. There are occasional examples when it is observed that one toad orients to the light much more slowly and hesitatingly than another. Some toads jump away from the light more rapidly than others and along a straighter path. There also is found to be variations in such responses on the part of the same animal on different occasions. These facts seem to indicate modifications in the bodily conditions of the animals concerned, especially when it is remembered that both the environment and the kind of stimuli remain unchanged. Loeb (*l.c.*, p. 24) and (1912, p. 47) early recognized the importance of differences in the physiological conditions of animals as modifying factors in animal responses. This subject has been discussed by the present writer (1912, pp. 281–283). It is not improbable, in the writer's experiments with young toads, that before orientation the animals are, as it were, in a condition of unstable equilibrium with reference to the light, and that the orienting response is one of adjustment; and further, after orientation is completed the toads are then in a condition of relative stability toward the light, so far as orientation is concerned, and they exhibit further response by jumping away from the source of illumination. With reference to orientation in general, may it not be a fact that previous to the orienting response the bodily state of the animal differs from its condition after orientation is complete?

The responses of young toads to the light from the projection lantern seem to indicate that the unequal light intensity on the two sides of the body is a factor in inducing the animals to orient so promptly and definitely. According to Holmes (1907, p. 346), frogs orient with respect to light in general in much the same manner. Pearse (*l.c.*, pp. 172–205) apparently takes a similar point of view with reference to the orientation of specimens (some of them immature) of *Bufo americanus* and *Bufo fowleri* to light of 220 ca.m. intensity (see particularly *l.c.*, pp. 204–205). The orientation of specimens of *B. ameri-*

canus (some of them immature), as described by Mast (*l.c.*, pp. 214–215, 219–220) appears to occur much in the same way as observed by the writer in young toads. The intensities of the lights employed by Mast in his experiments were 12.5 and 25 ca.m. It is probable, during the orienting response of young toads, that the light acts in some such manner as described by Loeb (1905, p. 32), and to which Mast (*l.c.*, p. 223) practically assents. Even so, though the light should act "at a constant intensity," such a fact does not necessarily preclude the influence of the differences in intensity on the two sides of the animal's body, during orientation.

In regard to the effect of light intensity upon the orientation of young toads, mention should be made of Mast's (*l.c.*, pp. 219–220) extremely interesting experiments with specimens of *Bufo americanus*, some being immature. Two lights of different intensities were employed, one being 12.5 ca.m. and the other 25 ca.m., and the source of illumination was two Nernst glowers, the two beams of light crossing at right angles. When a toad was placed, with one side turned toward the glower, in the beam of light of lesser intensity, it oriented directly and accurately, and then jumped toward the source of illumination. However, when the animal reached the intersecting beam from the light of greater intensity, instead of orienting toward this light, it continued to jump toward the weaker light. Altogether 42 trials were made, 36 of these being as described. In 6 cases only did the toad turn toward the stronger light when it reached the point of intersection of the two beams, and these six trials were all with the same individual. Seven toads only were used in the experiments. It would seem in a series of experiments exhibiting results of this nature that the effect of light intensity was modified as an orienting factor, or why did not the animals orient toward the light of stronger intensity. The present writer offers two suggestions which may prove to be partially, if not fully explanatory of this. First, the eyes are strongly stimulated by the light from in front, and the response to such stimulation in itself may result in producing an inhibitory effect upon the toad in so far as its response to the stimuli from the intersecting light is concerned. While it is true that in toads both skin and eyes are photoreceptors as Pearse (*l.c.*) has proved, it is evident that the cross rays from the stronger light

would reach one eye only with full effectiveness. Second, if animals with image-forming eyes go toward a source of light, because they perceive the light itself and follow it "much as an animal pursues any other object of interest" as indicated by Graber (*l.c.*, p. 248), Torelle (*l.c.*, p. 471), Holmes (1905a, pp. 341, 344–345) and (1908, p. 496), and Mast (*l.c.*, pp. 219, 223), then such behavior may present a partial explanation as to the reason why the toads used in Mast's experiments did not go toward the stronger light, for the "attention" of the animals may have been so fully occupied with the light in front of them that they did not turn into the intersecting beam, and jump toward the source of the stronger light. Further, it must be recalled, as Mast (*l.c.*, p. 223) himself has suggested, that the direction of the rays in the field may be a guidance to the toads, especially if they go toward an object because they see it. Then, the after effects of the directive weaker light may have been sufficient to keep the toads moving along the path already taken, even when they reached the strong intersecting beam of light. In so far as this work of Mast's applies to the writer's experiments with young toads, certain facts should be kept clearly in mind regarding the latter's experiments, that the animals employed were extremely immature, that light approximating 10,000 ca.m. intensity was used, and that the toads reacted negatively to the photic stimuli. From what is known of the habits of toads, it was to be expected that the animals would respond negatively to the strong stimuli from the projection lantern. Toads are very largely nocturnal animals, and are more commonly seen about twilight when they leave their places of "concealment," which they have occupied during the daytime.

The young toads respond positively to all the lesser light intensities of white light. In these experiments it seems as if the difference in the intensity of the stimuli on the two sides of the body was an important factor in orientation. This subject has been discussed in connection with the responses to the light from the projection lantern, and therefore will not be dwelt upon here. In jumping toward the light it is hardly probable that the rays *per se* in the field are a very important element in guiding the toads, for it has been stated that there must be many cross lights in the field of experimentation. Of course there is a certain part of Holmes's theory (1905, pp. 108–

109) that might apply here as a partial explanation, for a portion of the rays are parallel with each other and with the median longitudinal axes of the bodies of the toads. In the experiments in the dark room the principal object in the toad's field of vision is the light, and it is probable that the animals jump toward it because they see it, an idea that has been mentioned before. The light also may act continuously as Mast (*l.c.*) has suggested, and somewhat as Loeb (1890, p. 90) stated more than twenty years ago with reference to frogs when diffuse daylight was used as a stimulus. The following quotation gives Loeb's point of view:

> "Dass auch beim Frosch das Licht als konstante Reizursache wirkt, geht daraus hervor, dass die Thiere dauernd an dem der Lichtquelle entgegengesetzten Ende des Kastens sitzen bleiben."

In experiments with weak diffuse daylight, orientation is not a prominent feature in behavior, but there is some evidence of a tendency for the toads to gather toward the source of illumination.

Many of the responses of young toads to contact stimuli are probably adaptive ones, such as creeping under and between objects. Even so peculiar a response as that of the death-feint may be of such a nature, as the observations of some writers seem to indicate. It is true that in the case of some of the Arthropods, it is rather more difficult to see how the death-feigning response serves any adaptive purpose. The act of crouching against the ground and of inflating the lungs with air may be another example of a protective device. It would be of considerable scientific interest, for some investigator to make a long and varied series of observations with reference to the contact responses of young toads, and see in how many instances such responses were adaptive in function.

X. SUMMARY

Specimens of *Bufo americanus* Le Conte, approximately 14 mm. in length were collected near Ann Arbor, Michigan. They respond negatively to the light from a projection lantern, with an approximate illumination of 10,000 ca.m. within the field of experimentation. The animals jump away from the light toward the opposite end of the dish. If they are left in that

situation for some time, some of them climb up the perpendicular glass wall at the end of the vessel. This places them out of the most intense glare of the light. The young toads orient promptly and definitely, by turning away from the source of illumination and so place themselves that the longitudinal axes of their bodies lie parallel with the incoming rays. This position in relation to the rays of light is maintained while traveling from one end of the dish to the other, and the pauses between the jumps are brief, so that the animals move with a fair degree of speed. The responses in water are similar to those already described, the toads swimming away from the light.

The young toads respond positively to the light from a 16 c.p. incandescent light, with an illumination approximately of 44 ca.m. They also respond in a similar manner to strong diffuse daylight, to weak diffuse daylight, and to sunlight. Except in the case of diffuse daylight, the animals jump toward the source of illumination in a comparatively straight path. It cannot be said that the median longitudinal axes of the bodies of the toads are parallel with all the incoming rays, because many of the rays enter the experimentation dish at various angles and there must be cross lights within the field of experimentation. While the animals jump toward the light with considerable promptness, their motor responses are perhaps not so quick as in the experiments with the projection lantern. At times it seems as if the toads do not travel in quite so straight a path as is the case when the intense artificial light is used as a source of stimulation. The toads orient fairly definitely and accurately, but not so promptly as when the projection lantern is employed. At times, when responding to sunlight, the animals come to rest in diffuse daylight, if it is nearby. Neither the movement toward the light nor the orientation is so definite as in the case of the stronger intensities.

It is not improbable that both light intensity and ray direction in the field are factors in these photic responses. During orientation light intensity may play the more important rôle, while the rays in the field may act as a guiding factor after orientation is complete, though this does not necessarily do away with the effect of intensity. In the positive responses vision is an element not to be ignored, and it is probable that

the light acts continuously. Further, it is not impossible that a modified form of "trial and error" may function as the animals travel toward or away from the source of illumination. In the experiments with weak diffuse daylight, ray direction in the field probably exerts comparatively little influence upon young toads.

Young toads react to light passed through red and blue solutions by giving motor responses. When red light is employed singly, it is noticed that the stimuli are not very effective. There is a tendency for the animals to act negatively, both by turning and jumping away from the light. The responses are less definite than when either white or blue light is used. When blue light is employed the toads both turn and jump toward the light, and they do so with more promptness, than is the case when red light is used. When red and blue lights are used at the same time, more animals jump toward the blue light than they do toward the red light. Some toads jump toward the red light, and a few individuals appear to be indifferent.

Young toads subjected to light react to contact stimuli by giving the motor response. If a stationary individual is stimulated by another animal jumping against it, the former responds either by turning or by jumping away. Frequently after such a motor response, the animal follows it up by reacting to the light. In the experiments with the lesser light intensities, the young toads may respond to contact by several of them gathering in the angles formed by the bottom and sides of the experimentation dish. They remain in such situations with their bodies in close contact.

Young toads frequently react with the death-feigning response when handled with undue pressure and roughness. During such response they remain immobile, with their legs drawn up against the body. A toad may be caused to respond in this manner by placing the animal on its back and holding it in that posture for a few seconds. The length of the death-feint varies in different individuals. If a toad has been made to feign death in diffuse daylight, the response may be curtailed by suddenly flashing a beam of light from the projection lantern upon the animal. Young toads usually arouse from the death-feint abruptly. A sudden tactual stimulus will effect this. The death-feigning response may probably result in producing

a bodily condition in young toads not far removed from that of hypnosis described by Verworn in other animals.

Young toads will also respond to contact in another manner. Sometimes when touched the body is pressed closely against the ground, and the lungs are inflated with air, the head also being bent downward. While in this position an animal remains motionless. It is likely that many of these responses to contact on the part of young toads are adaptive in function.

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THE STIMULATION AND THE INHIBITION OF OVULATION IN BIRDS AND MAMMALS

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A previous article (Craig, 1911) by the present writer showed that in six cases female Ring-Doves (*Turtur risorius*) were induced to lay by the courting behavior of male doves though the introduction of sperm was prevented. And in one case a female dove laid her eggs in due time after being stimulated merely by a human being who spoke kind words to her and stroked her head and neck in a friendly way. The opinion was expressed that this last experiment could be repeated if one could get a dove sufficiently tame and willing to show courting behavior toward a human being, as doves sometimes do.

This expectation was fulfilled in the year 1911, with dove No. 41, a young female which had been reared in isolation, which therefore had had no experience with a dove mate, but regarded human beings as her companions. Human beings were kept away from her cage so far as possible until April 25, when the experimenter suddenly began to spend much time near her cage, to put his hand in the cage, and sometimes to preen her head and neck. The dove began next day to respond to the hand with nest-calling behavior (though she was given no nest) and on May 3 she laid her egg. I now find, too, that the same experiment was performed centuries ago by Harvey, on a parrot. "Harvey records that, by stroking the back of a favorite parrot (which he had possessed for years and supposed to be a male), he not only gave the bird gratification,—which was the sole intention of the illustrious physiologist,—but also caused it to reveal its sex by laying an egg." (Robinson, 1892, p. 1295).

It is well known to pigeon breeders that two female pigeons kept together may mate and lay eggs. Some experiments have been made by the writer in mating a female Ring-Dove with another female. In all such cases the two females have gone through a courting performance and in due time both have laid eggs; and after a period of incubation they have repeated the

courting performance and the egg-laying. This was observed in the year 1911 in two cases, and in 1912 in twenty-four cases, involving six birds. A very significant detail is, that as the three pairs of females in 1912 were kept in one room, with no other birds in the room, the three pairs showed a marked tendency to keep time with each other in their laying. Each pair could not see the other pairs, but when they heard their excited cooing and kahing and running about, the tardiest pair were thereby stimulated and brought into similar activity.

The mate is not the only environmental factor in determining the time of egg-laying in the dove. As Professor Whitman said to me: "A great many factors enter in. Even if the female has the male, if she has no nest box and no nesting conveniences she may not lay. The egg develops and passes down the oviduct by degrees corresponding to the whole activity of the pair. It takes a week to ten days (in the domestic pigeon). This is true whether the pair are building their first nest or are preparing for a second brood. If, when the female is ready the male is not, she waits for him." In order to prevent birds from laying too late in autumn or too early in spring, Professor Whitman found that it was not always necessary to separate the sexes: he could keep mates together but with no nesting facilities, nothing to "go to work with," and this prevented their breeding. An excellent account of this matter is to be found in a paper by Harper (1904). That the female pigeon will refrain from laying if conditions do not satisfy her, has been so long known to breeders that it is mentioned by Aristotle (1891), who says, "Pigeons are able to retain their eggs even in the act of parturition. If they are disturbed by anything occurring in the neighbourhood of their nest, or a feather be plucked out, or if anything else troubles or disturbs them, they retain the egg they were about to lay." In two cases among my doves this year I observed a bird hold back her egg at the time of parturition, because she was kept away from her nest. However, when the egg is fully developed and ready to lay, the bird's power to retain it is evidently limited. The real control of the production of eggs is earlier, connected with the ovary itself and the process of ovulation.

Professor Whitman had one season a solitary female American robin, which built a nest by herself and laid a set of eggs in it.

This is a familiar occurrence in many species of birds. In such cases it is sometimes assumed simply that the maturing of eggs is the cause of the nest-building. But the reverse is no doubt equally true; the activity of building and the contact with the comfortable nest stimulate the development of eggs. The visceral and the peripheral activities of the bird are in reciprocal relation; each stimulates the other, and they proceed step by step together. It is a case of "circular activity" (Baldwin, 1906). Contact with the nest, under appropriate conditions, exerts a powerful suggestive or an almost hypnotic influence upon the bird, causing in her an emotional attitude which somehow involves the ovaries. This attitude leads her to work further upon the nest. Such work causes the stimulus from the nest to be repeated. Thus the circular activity goes on and on.

In the paper on the influence of the male on ovulation, I said (Craig, 1911, p. 300): "The influence of the male in inducing oviposition is a psychological influence." The reviewer of that paper in the Psychological Bulletin (Washburn, 1912, p. 309) says: "The word 'psychological' is perhaps a little extreme here: the tactile stimuli produced by the male's preening of the head and neck of the female might operate reflexly." No doubt a reflex arc is involved here as in all nervous action; but it is not a simple reflex. It is a reflex which is set working, not by any one sense stimulus, but by the total situation including both the totality of present sense stimuli and also memory factors.

The one condition necessary to induce ovulation is that the female should accept the attentions paid to her and throw herself into the mating and laying attitude.[1] When she does so, her whole organism is affected. Her posture in standing and her carriage in walking are greatly altered. She follows the male to the nest and spends hours in dedicating and building that structure (whereas a solitary female pays no attention to a nest, under normal conditions). Her whole bearing shows intense emotion, not violent, but deep. As the days pass, this manner grows upon her, becoming an extreme attitude at the time of egg-laying.

[1] The mating and the laying attitudes may be said to be two attitudes which are subdivisions of one more general. In the ordinary course of the brood cycle, the two are closely united. But I think I have seen each occur quite without the other. In Case 2 (Craig, 1911), for example, there seemed to be no mating attitude whatever, only a laying attitude.

This great transformation is determined by the entire social situation which changes the dove from the status of the unmated (or it may be from some other stage in the brood cycle) to the status of matehood. No one factor determines it—not the mechanical stimulation of the neck feathers, nor the act of billing (which was one of Harper's suggestions), nor even copulation. As to the preening of the neck feathers: I once tried persistently preening the neck feathers of a dove which refused to accept such action as from a mate: she showed no laying attitude and laid no eggs. A dove which has been abruptly separated from her mate and given a strange male, though that male preens her neck feathers and plays up to her perfectly, may remain quite unstimulated. Conversely, the females which were paired with their own sex, as above mentioned, preened one another very little as compared with males; yet they accepted each other as mates, and they laid eggs. As to billing: These females mated with females again illustrate, for they billed but little and imperfectly, in some cases not billing at all. And in the case of the birds induced to lay by hand, there was of course complete absence of billing. As to copulation: That this is not a necessary factor is proved by the cases in which the female was induced to lay by preening the feathers of the head and neck. Bartelmez (1912, p. 290) mentions that a female may lay even when the male stimulating her is in another cage. Conversely, there are cases in which a pair copulate regularly, yet the female does not lay. And in some such cases the cause seems unquestionably to be that the female is dissatisfied, as with her nest or other circumstances, hence does not get into the laying attitude above described, and consequently does not ovulate. I think that in some, though not in all cases, one could prevent ovulation in a mated female by persistently following her and turning her out of any corner where she began to settle in the laying attitude.

Data which will be given at length in other articles, show that there is a difference in this respect between young doves which have never mated and old doves which have been breeders for years. The inexperienced are more ready to enter into abnormal matings,—as, with their own sex, or with alien species, or with the hand,—or to lay without a nest. They lay eggs in conditions under which an old experienced dove would

refuse to do so. Indeed, the assumption of the egg-laying attitude is, to a limited degree, a voluntary activity (if the word voluntary may be applied to animal activities), for it depends upon the dove's disposition, her whole past history, and her whole attitude toward the present situation.

Just as certain environmental conditions stimulate egg-laying, so there are certain environmental conditions which inhibit it. Some of the facts already given illustrate such inhibition. A clear case of it is seen in species of birds of which the female tends to lay eggs continuously until they reach a certain number, the sight of which (or the touch?) inhibits further laying. Egg collectors have often caused such a bird to lay an abnormally large number of eggs, by leaving only one "nest egg" in the nest, removing every additional egg as soon as it appears. Perhaps the most remarkable instance recorded is that of a flicker (*Colaptus auratus*) experimented on by Mr. Charles L. Phillips, of Taunton, Mass. "On May 6, 1883, he found a cavity in a large willow tree containing two eggs; he took one, leaving the other as a 'nest egg,' and continued to do so day after day until the female flicker had laid seventy-one eggs in seventy-three days." (Davie, 1898.)

Columbidae do not prolong their laying in this manner. In them, the number of eggs in a set is predetermined in the ovary, and is never more than two. But it is clear that all through the incubation period the presence of eggs in the nest prevents the ripening of the new set of ova, which will ripen as soon as the bird reassumes the laying attitude. That the sight of eggs in the nest can inhibit the assumption of the mating attitude, is shown by the following scene, which is familiar to every keeper of pigeons or doves: The hen dove is sitting on her eggs; her mate comes to her with bowing coo and other signs of intense excitement; she is gradually aroused, rises, shows a mating attitude, and starts to leave the nest; then she catches sight of the eggs, and as she looks at them her attitude changes toward that of brooding; she stands hesitant for several seconds, drawn one way by the stimulus from the mate and the other way by the stimulus from the eggs; gradually the brooding attitude becomes stronger, the mating attitude disappears, she goes back and settles on the eggs. But if now the eggs be removed from the nest, the hen dove loses her brooding attitude, and it

may be, as Professor Whitman observed, only a half hour until the birds are at work preparing for another laying.

When wild birds (and other animals) kept in captivity refuse to breed, the trouble in many cases is surely psychological. It is not that the birds are in poor health, or have improper food, etc. It is that the conditions fail to stimulate or even positively inhibit the arousal of their breeding instincts and of the associations formed during their wild breeding experience.

Between the different species and different orders of birds there are great differences in the relation of ovulation to environmental conditions. The stimulation of ovulation by the social activity of the male occurs no doubt in all the Columbidae and probably in a great many other monogamous birds. The domestic fowl and perhaps all the Phasianidae (Craig, 1911; Harper, 1904, p. 353) present an extreme contrast to the pigeons, in that their ovulation is highly independent of mating. Parasitic layers such as the European Cuckoo and the North American Cowbird (*Molothrus ater* Bodd) are probably descended from forms whose ovulation resembles that of the pigeon, but have evolved to a state in which ovulation is more independent of environment, at least not depending upon any stimulus of the bird's own nesting activity. This is in agreement with the conclusion of Herrick (1910, p. 232) that the habit of parasitic laying is connected with a disturbance of the "attunement of egg-laying to nest-building."

Harper (1904, p. 352) hinted that what we have said of pigeons does not apply at all to the Mammalia, that in the latter ovulation is "exclusively a female function." But this is an error. It has been shown for many Mammals (Thomson, 1839, p. 44; Marshall, 1910, pp. 134–139; Longley, 1910) that ovulation is favored by or may even depend upon union with a male. And there is reason to believe that what is true of pigeons is true also of these mammals: that in so far as ovulation is dependent upon environment, it is dependent, not upon any one afferent stimulus, but upon the entire situation—involving the female's inborn disposition, her whole past history (see pp. 215–218) and all factors in the present environment which affect the social, emotional situation.

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SOME REFLECTIONS ON THE ORIGIN AND SIGNIFICANCE OF THE CEREBRAL CORTEX

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Four figures

What are the elements of consciousness? Psychologists used to talk about simple sensations, elementary feelings and pure volition, but most of us have difficulty in finding these things introspectively. Our sensations and volitions are inextricably interwoven with each other and with ideas of various grades of complexity. The child is born with definite physiological capacities for reflex response to stimuli and with certain impulses and instinctive tendencies, none of which necessarily involve any conscious element. On this foundation he builds up by slow increment his mental life.

The intellectual superstructure is not built up out of simple sensations, which are first compounded into perceptions and then disembodied as ideas; quite the contrary, the child's first experiences are with completed physiological circuits, kicking, sucking and the like, and these are soon elaborated in accordance with his innate impulsive and instinctive endowment into complex behavior types, which are rapidly modified by experience. The mental elements, from the genetic point of view, are to be sought in these behavior complexes, rather than in any abstractions derived by a process of logical analysis from philosophical postulates or highly sophisticated adult introspection.

What these first mental elements may be in the very young child it is impossible for a man (even though he be a psychologist) to determine by any simple method; but many of our adult mental processes arise apparently immediately from a conflict of two or more instincts or automatisms no one of which would necessarily by itself have any mental content. And these mental processes in turn resolve themselves into action and run down into automatism again.

The plain man who is not versed in the subtleties of philosophical dialectic or introspective analysis is apt to conclude that

the units which we recognize in consciousness in the simplest mental processes which we can observe are not simple elements at all, but complexes of sensation, feeling, impulse, or what-not, whose character is in some measure predetermined in each case by the organization of the physiological circuit with which it is genetically related. Without attempting here a justification of this conclusion on psychological grounds, let us inquire how it accords with what we know of cerebral structure.

There are no afferent tracts leading to the cerebral cortex directly from any peripheral sense organ or from any center within the brain which is "pure," i.e., devoted to a single sensory function. In other words, no simple sensory impulses ordinarily reach the cortex, but only nervous impulses arising from lower correlation centers, where complex reflex combinations of various sensory systems are possible. The optic impulses reach the cortex most nearly pure, i.e., with less subcortical associational relation with other sensory systems (it is no accident that the visual sense plays a dominant rôle in human cortical function);[1] but even here the optic centers in the thalamus from which the optic projection fibers arise are intimately related with acoustic, tactile and other important sensory centers. And in the case of all of the other sensory systems, the projection fibers which enter the cortex come from centers which are separated from their respective sense organs by two or more association centers of a high order of complexity. Each of these subcortical associational centers may be dominated physiologically by a single sensory system, but it is structurally adapted for bring-

[1] The optic apparatus is peculiar in that the cortical optic path, instead of first passing through the lower reflex centers (optic tectum) on its way to the thalamus, as in the case of the other sensory systems, is short-circuited in the pulvinar and lateral geniculate body before the mesencephalic centers for the simpler optic reflexes are reached. Sherrington's researches on sensual fusion (Integrative Action of the Nervous System, chap. 10) have shown that the sensory stimuli received from each eye are independently elaborated subcortically, but that the fusion of the uniocular sensation complexes into a single mental image is cortical. "The binocular combination must be a synthesis of a left eye with a right eye *sensation.*" "The singleness is therefore the product of a synthesis that works with already elaborated sensations contemporaneously proceeding" (p. 383). The separateness of the cerebral processes for the two eyes is probably correlated with the necessity for accurate spatial localization in the field of vision. Similarly, some elements of cutaneous sensibility, where accurate spatial localization in consciousness is also highly developed, reach their thalamic centers very directly through the medial lemniscus (Head and Holmes, Brain, vol. 34, 1911), while others pursue a more indirect route through the lateral lemniscus, the latter type of connection being the more primitive.

ing that system into relation with several others, so that the nervous discharge which emanates from it may be the efferent link in a very complex reflex arc. This efferent discharge may descend to the appropriate motor center, or it may ascend to enter a still higher association center, all of whose afferent tracts come from similar lower centers and therefore carry nervous impulses which represent a sort of physiological resultant of the functional factors there interacting.

A few selected illustrations of the various types of correlation centers may clarify these relations. Fig. 1 illustrates the simplest reflex arc. An auditory impulse coming to the brain terminates in a primary acoustic center in the superior olive,

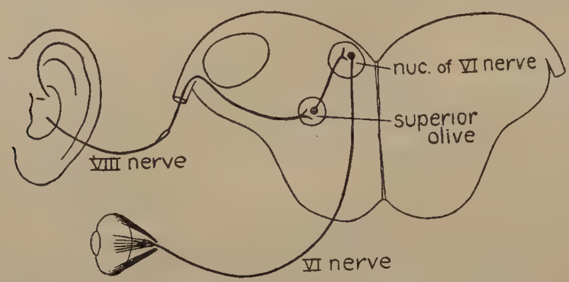

FIGURE 1.—Diagram of a simple auditory reflex. Upon stimulation of the endings of the VIII nerve in the ear by sound waves, a nervous impulse may pass to the superior olive, whence it is carried by an intercalary neurone of the second order to the nucleus of the VI nerve. The fibres of this nerve end on the external rectus muscle of the eyeball.

where it is taken up by an intercalary neurone and transmitted to the nucleus of the VI nerve. The result is a contraction of the external rectus muscle of the eyeball, turning the eye toward the side from which the auditory stimulus was received. (There is another path leading to the nucleus of the III nerve for the innervation of the internal rectus muscle of the other eye, thus providing for conjugate movements of the two eyes—but that is another story.) This reflex arc operates *per se* in a purely mechanical fashion to produce a determinate invariable type of response.

Other fibers arising in the primary acoustic center may ascend to the roof of the midbrain (corpora quadrigemina), where they are brought into relation with fibers belonging to other functional systems. In the lower amphibian brains (e.g., the com-

mon mud-puppy, Necturus) this associational mechanism is the simplest possible (Fig. 2). Here the upper part of the midbrain roof receives optic fibers from the optic tracts, while the lower part receives lemniscus fibers from the primary acoustic and tactile centers. A single neurone of the midbrain may send one dendrite upward to receive optic stimuli and another dendrite downward to receive acoustic or tactile stimuli (or both of these). If the animal receives visual and auditory stimuli simultaneously, the intercalary neurone of the midbrain may be excited by both sets of stimuli. Its discharge through the

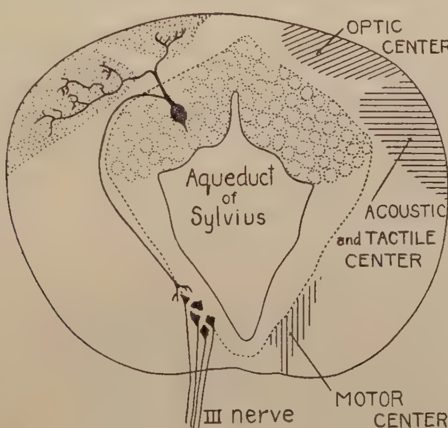

FIGURE 2. Diagram of a cross-section through the midbrain of Necturus, illustrating a single association neurone of the midbrain roof. One dendrite spreads out in the optic center among terminals of the optic tracts; another dendrite similarly spreads out in the acoustic and tactile center. The axon descends to connect with the motor neurones of the third nerve.

axon to the motor organs of response (say to the eye-muscles by way of the third nerve, as in Fig. 2) will be the physiological resultant of both sets of excitations. If they reinforce each other, the discharge will be stronger and more rapid; if, on the other hand, they tend to produce antagonistic responses, there will be an inhibition of the response or a delay until one or the other stimulus obtains the mastery.

In the human brain the corresponding structures are similar in functional type, but much more complex, with many systems of intercalary neurones between the different functional centers. The midbrain roof (corpora quadrigemina) is differentiated into

a superior colliculus for optic impressions and an inferior colliculus for auditory impressions, with a complicated system of associational neurons putting these secondary centers into physiological relation. But the final motor discharge in each case may be the result of the reaction of the whole apparatus and not of either the optic or the auditory center alone.

A further complication arises from the fact that the efferent tract is not simple, as diagrammed in Fig. 2; but it divides into a descending and an ascending path. The former connects directly with motor centers, including the oculo-motor, bulbar and spinal motor nuclei, while the latter enters the thalamus, where associations of a still higher order are effected (Fig. 3).

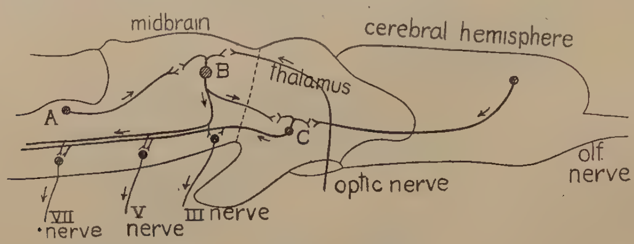

FIGURE 3. Diagram of some conduction paths in the brain of Necturus, seen in longitudinal section. From the medulla oblongata an acoustic impulse may be carried forward through the neurone *A* to the midbrain, whose neurones, *B*, are of the type shown in Fig. 2, receiving both acoustic and optic impulses. This neurone *B* may discharge downward to the motor nuclei of the III, V, VII, etc., nerves, or it may discharge upward to a neurone of the thalamus, *C*, which also receives descending impulses from the cerebral hemisphere.

Here is introduced a physiological choice or dilemma; the response is not a simple mechanical resultant of the interacting stimuli, but its character may be influenced by variable physiological states. The determinate type of action is replaced by a relatively indeterminate or labile type. In the thalamus the nervous impulse is again subjected to modification under the influence of a still greater variety of afferent impulses, for these centers receive all sensory types found in the midbrain, and in addition important descending tracts from the cerebral hemispheres—in lower vertebrates the latter are chiefly olfactory. In fishes and amphibians few optic fibers enter the thalamus directly, but most of these pass by to end in the midbrain.

The fibers which enter the thalamus in general come from other association centers and therefore may carry impulses which have been already elaborated into rather complex systems of

reflexes, rather than simple sensory elements. In the thalamic centers these reflex systems in turn become the units involved in a further process of coördination, the resultant responses being still further removed from the rigidly determinate type of response characteristic of the simple reflex arc. The efferent neurons of the thalamus, like those of the midbrain, discharge into the cerebral peduncles and lower motor centers, but the reflex and instinctive responses thus brought to pass are of a more complex sort than those of the primary and secondary correlation centers of the medulla oblongata and midbrain, and are far more easily modifiable by experience and by variable physiological states.

The thalamus of lower vertebrates (say all species below the frog) is probably the organ of the highest associations of which these animals are capable. These are mostly on the reflex and instinctive plane, though of course a limited psychic factor cannot be excluded. The cerebral hemisphere of fishes is dominated by the olfactory system, as the midbrain is by the optic system, and, so far as may be inferred from the anatomical evidence, is by no means so efficient an associational mechanism as the thalamus. There is nothing in these animals which can be compared, when physiologically considered, with the mammalian cerebral cortex, though the primordia from which that cortex has been derived in higher animals can be readily identified in them. It is indeed clearly established that the hippocampal formation (archipallium) has been differentiated from the dorso-medial segment of the wall of the primitive cerebral hemisphere, while the rest of the cortex (neopallium) was elaborated from materials found in the lateral wall of the hemisphere, the somatic area of Johnston. But in fishes and the lower amphibians there is nothing here which conforms to our ideas of cerebral certex, either structurally or functionally considered.

It is a far cry from an identification of the topographic sources of the structural material from which the cerebral cortex has been gradually elaborated to an adequate understanding of the functional factors which have effected that differentiation. As well might one say that the discovery of the quarries from which the materials for the Parthenon were dug would give an adequate explanation of that architectural masterpiece.

Starting from the very primitive "somatic area" of fishes, we can trace in amphibians, reptiles, birds and mammals the gradual differentiation of the non-olfactory parts of the cerebral hemispheres. In the initial stages of its evolution this structure is organized much like the thalamus. It receives no afferent fibers which come directly from any simple primary sensory center, but only fibers from association centers of the second or third order, which are themselves capable of elaborating complicated reflex responses.

The thalamus, as we have seen, has its own intrinsic system of association centers, which discharge downward into the cerebral peduncles, and this is the primary reflex apparatus of this part of the brain. The thalamo-cortical connections arose to prominence later in the evolutionary history, though feeble rudiments of these are present in lower brains. Parallel with the enlargement of these cortical connections a special part of the thalamus was set apart for them and from the Amphibia upward in the animal scale this dorsal part of the thalamus assumed increasingly greater importance. This part is termed by Edinger the neothalamus and makes up by far the larger part of the thalamus in the human and all other mammalian brains. It occupies the dorsal part of the thalamus proper and comprises most of the great thalamic nuclei (anterior, lateral and ventral nuclei, pulvinar and lateral and medial geniculate bodies). The primitive intrinsic reflex thalamic apparatus in man is a relatively unimportant area of medial grey matter and the subthalamic region (corpus Luysii, lattice nucleus, etc., not to be confused with the hypothalamus which lies farther down in the tuber cinereum and mammillary bodies).

The neothalamus, accordingly, serves as a sort of vestibule to the cortex, every afferent impulse from the sensory centers (except the olfactory system) being here interrupted by a synapse and opportunity offered for a wide range of subcortical associations. The olfactory cortex (hippocampal formation) has a similar relation to subcortical correlation centers in the olfactory area in the anterior perforated space, septum, etc.

From these anatomical considerations it follows that no simple sensory impulse can, under ordinary circumstances, reach the cerebral cortex without first being influenced by subcortical association centers, within which complex reflex combinations

may be effected and various automatisms set off in accordance with their preformed structure. These subcortical systems are to some extent modifiable by racial and individual experience, but their reactions are chiefly of the determinate or stereotyped character, with a relatively limited range of possible reaction types for any given stimulus complex.

It is shown by the lower vertebrates which lack the cerebral cortex that these subcortical mechanisms are adequate for all of the ordinary simple processes of life, including some degree of associative memory. But here, when emergencies arise which involve situations too complex to be resolved by these mechanisms, the animal will pay the inevitable penalty of failure—perhaps the loss of his dinner, or even of his life.

In the higher mammals with well developed cortex the automatisms and simple associations are likewise performed in the main by the subcortical apparatus, but the inadequacy of this apparatus in any particular situation presents, not the certainty of failure, but rather a dilemma. The rapid preformed automatisms fail to give relief, or perhaps the situation presents so many complex sensory excitations as to cause mutual interference and inhibition of all reaction. There is a stasis in the subcortical centers. Meanwhile the higher neural resistance of the cortical pathways has been overcome by summation of stimuli and the cortex is excited to function. Here is a mechanism adapted, not for a limited number of predetermined and immediate responses, but for a much greater range of combination of the afferent impressions with each other and with memory vestiges of previous reactions and a much larger range of possible modes of response to any given set of afferent impressions. By a process of trial and error, perhaps, the elements necessary to effect the adaptive response may be assembled and the problem solved.

It is evident here that the physiological factors in the dilemma or problem as this is presented to the cortex are by no means simple sensory impressions, but definitely organized systems of neural discharge, each of which is a physiological resultant of the reflexes, automatisms, impulses and inhibitions characteristic of its appropriate subcortical centers. The precise form which these subcortical combinations will assume in response to any particular excitation is in large measure determined by the

structural connections of these centers *inter se*. And the pattern of these connections is tolerably uniform for all members of any animal race or species. This implies that it is hereditary and innate. This is the underlying basis of instinct.

The connections between the cortical centers, on the other hand, are much less definitely laid down in the hereditary pattern. The details of the definitive association pattern of any individual are to a greater degree fixed by his particular experience. This is the basis of docility and the individually modifiable or intelligent types of behavior. The typical cortical activities, even when physiologically considered, are far removed indeed from those of the brain stem.

It should be emphasized, however, that the differences between the cortex and the lower centers of the brain stem, so far as these can be deduced from a study of structure and from physiological experiment, are relative and not absolute. Indeed the general pattern of the regional localization of the cortex itself is innate and in adult life the cortex has acquired many more characteristics similar to those of the brain stem, with its own systems of acquired automatisms and habitually fixed types of response. The larger asscciation centers retain their plasticity longest, but ultimately these also cease to exhibit new types of coördination and this marks the onset of senility.

The cerebral cortex, then, is not to be likened to the seat of an absolute monarch who receives his messages from outlying parts of his empire in the form of simple sensations and executes his will directly upon his subjects, the bodily organs; but rather to an upper house of parliament with limited powers of initiating legislation *de novo*, but with remarkably extensive capacity for the revision and amplification or veto of such bills as are sent up to it from the lower house and with a very efficient direct control over the entire administrative machinery of the government.

Dewey's stimulating analysis[2] of the reflex arc concept, or as he prefers to say, the organic circuit concept, implies that the synthesis of the elements of a complex chain reflex into an organic unity is the essential prerequisite of that apperceptive

[2] The Reflex Arc Concept in Psychology. *Psych. Rev.*, vol. 3, p. 357, 1893. See also Dewey's later statement in *Jour Philos., Psych. and Sci. Methods*, vol. 9, Nov., 1912, pp. 664–668, especially the footnote on p. 667.

process which will make the total experience of value for future discriminative responses — for learning by experience. This, which is true in the individual learning process, is also true phylogenetically. The coördination centers (and their capacity for the preservation of vestiges of past reactions) are the organic mechanism for this synthesis. They make it possible that a new stimulus may be reacted to, not as a detached element, but as a component of a complex series of past and present adjustments, to which it is assimilated in the association centers—apperception. This assimilation or apperceptive process is an integral part of the receptor process in the higher centers, giving the quale to the idea of the exciting object. Cotemporaneously with this stimulus-apperception process we have an apperception-response-activity giving the object-or purpose-idea, so that the entire reaction is to be regarded as stimulus-apperception-response, as a functional unity rather than as a sequence: stimulus > apperception > response.

Dewey's organic circuit concept is elaborated in terms of psychology. Let us see how it may be applied to biological behavior.

The simple reflex is commonly regarded as a causal sequence: given the gun (a physiologically adaptive structure), load the gun (the constructive metabolic process), aim, pull the trigger (application of the stimulus), discharge the projectile (physiological response), hit the mark (satisfaction of the organic need). All of the factors may be related as members of a simple mechanical causal sequence except the aim. For this in our illustration a glance backward is necessary. An adaptive simple reflex is adaptive because of a pre-established series of functional sequences which have been biologically determined by natural selection or some other evolutionary process. This gives the reaction a definite aim or objective purpose. In short, the aim, like the gun, is provided by biological evolution and the whole process is implicit in the structure-function organization which is characteristic of the species and whose nature and origin we need not here further inquire into.

Now passing to the more complex instinctive reactions, so far as these are unconscious automatisms, they may be elaborations of chain reflexes of the type discussed above (Loeb). But the *aim* (biological purpose) is so inwrought into the course

of the process that it cannot be dissociated. Each step is an integral part of a unitary adaptive process to serve a definite biological *end*, and the animal's motor acts are not satisfying to him unless they follow this predetermined sequence, though he himself may have no clear idea of the aim.

These reactions are typically organic circuits. The cycle in some of the instincts of the deferred type comprises the whole life of the individual. In other cases the cycle is annual (as in bird migrations, etc.), diurnal or linked up with definite physiological rhythms (e.g., the nidification of birds as described by F. H. Herrick[3]). In still other cases there is no apparent simple rhythm. But always the process is not a simple sequence of distinct elements, but rather a series of reactions, each of which is shaped by the interactions of external stimuli and a preformed or innate structure which has been adapted by biological factors to modify the response to the stimuli in accordance with a purpose, which from the standpoint of an outside observer is teleological, i.e., adapted to conserve the welfare of the species.

Every intelligently directed response to external stimulation involves a large measure of highly complex unconscious cerebration of this type; and it is possible to describe with considerable precision the mechanisms of the subcortical activities involved in many of those organic circuits which are commonly regarded as typically cortical.

Much of that which goes in psychological literature under such contradictory terms as unconscious mind or subconscious mind is in reality the subcortical elaboration of types of action system which ordinarily do not involve the cortex at all but which upon occasion may be linked up with cortical associational processes and then come into consciousness in such a form as to suggest to introspection that they are all of a piece with the conscious process with which they are related. In fact, within the cortex itself there are doubtless many routine activities which do not ordinarily come into consciousness, particularly of the sort known as acquired automatisms or lapsed intelligence; and these, though of quite different origin from the innate instinctive systems, cannot easily be distinguished from them in the form in which they are experienced in the adult.

[3] *Science*, N. S., vol. 25, 1907, pp. 725-726 and 781-782.

In the organic circuit as defined by Dewey the process is considered as a whole so that the response is conceived as logically implicit in the stimulus. The motor reaction, he says, is not merely *to* the stimulus; it is *into* the stimulus. "It occurs to change the sound, to get rid of it." "What we have is a circuit, not an arc, or broken segment of a circle. This circuit is more truly termed organic than reflex, because the motor response determines the stimulus, just as truly as sensory stimulus determines movement." This notion, which is difficult for the practical scientific mind to understand, is considerably clarified by some neurological considerations.

From the standpoint of the cerebral cortex considered as an essential part of the mechanism of higher conscious acts, every afferent stimulus, as we have seen, is to some extent affected by its passage through various subcortical association centers (i.e., it carries a quale of central origin). But this same afferent impulse in its passage through the spinal cord and brain stem may, before reaching the cortex, discharge collateral impulses into the lower centers of reflex coördination, from which incipient (or even actually consummated) motor responses are discharged previous to the cortical reaction. These motor discharges may, through the "back-stroke" action, in turn exert an influence upon the slower cortical reaction. Thus the lower reflex response may in a literal physiological sense act *into* the cortical stimulus complex and become an integral part of it.

But there is another aspect of the problem which has recently been brought to our notice by Kappers.[4] It is a well known fact, which is not often taken account of in this connection, that the descending cortical paths (central motor bundles) do not typically end directly upon the peripheral motor neurones whose functions they excite, but rather upon intercalary neurones which lie in the reticular formation or even in the adjacent sensory centers. These intercalary neurones in turn excite the peripheral motor neurones. The same intercalary neurone which receives the terminals of the pyramidal tract also receives collaterals from the peripheral sensory neurones of its own segment (Fig. 4). This arrangement is the explanation of the fact that

[4] Kappers, C. U. Ariëns. Ueber die Bildung von Faserverbindungen auf Grund von simultanen und sukzessiven Reizen. Bericht über den III. Kongress für experimentelle Psychologie in Frankfurt a. Main, 1908. Also, Weitere Mitteilungen über Neurobiotaxis. Folia Neuro-Biologica, Bd. I, No. 4, April, 1908, pp. 507–532.

the pyramidal tract fibers descend through the human spinal cord for the most part in the dorso-lateral columns, not in the ventral columns like most other motor tracts. In most lower mammals the pyramidal tract actually descends within the dorsal funiculus in the closest possible association with the peripheral sensory fibers, and this arrangement is clearly the primitive relation of the descending cortical pathway.

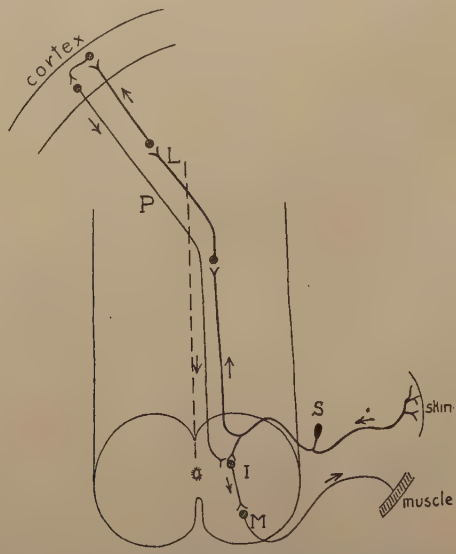

FIGURE 4. Diagram of the relations of the pyramidal tract in a rabbit or similar lower mammalian brain. Sensory stimuli enter the spinal cord from the skin through the peripheral sensory neurone, *S*, and ascend to the cerebral cortex through the lemniscus, *L*. The descending pyramidal tract, *P*, lies in the dorsal funiculus of the spinal cord. Its intercalary neurone, *I*, may be stimulated by both the peripheral neurone *S* and by the pyramidal tract *P*. It discharges upon the peripheral motor neurone, *M*.

Accordingly, stimulation of the skin of the body excites a dorsal spinal root fiber which ascends toward the cortex within the spinal cord and also gives collateral branches to intercalary neurones of the spinal cord itself. The latter neurones may excite motor elements of the spinal cord to an immediate reflex response which is well under way before the cortical return motor impulse gets back to the spinal cord and discharges into these same intercalary neurones which are already under sen-

sory stimulation directly from the periphery. The effect of this arrangement is that the central motor path during function is under the influence of sensory stimulation at both ends, and is not, as commonly described, under simple sensory stimulation at the cortical end and purely emissive in function at the spinal end.

Viewed from the standpoint of cerebral dynamics, the exact physiological effect of the discharge of a central motor bundle such as the pyramidal tract will be dependent upon the combined action of the sensory stimulation at the cortical end and the state of sensory excitation at the spinal end, as well as upon the resistance of the motor apparatus itself.

We saw in a previous paragraph how the simple reflexes of the spinal cord may become factors in the stimulus complex of the cortex. Here we find, conversely, that the efferent cortical discharge may become a factor in the local reflex stimulation of a motor spinal neurone. From both standpoints, Dewey's conception of the unitary nature of the organic circuit, as contrasted with the classical reflex arc concept, receives strong support.

The thalamic association centers probably serve as the organs *par excellence* where are elaborated those organic circuits which give to the higher apperceptive processes of the cortex that quale to which Dewey refers. The origin of this quale is to be sought partly in the subcortical assimilation of a present stimulus complex to the pre-existing organic circuits structurally laid down in the reflex mechanism, and partly in an affective quality pertaining to the several organic circuits involved in the reaction. This affective quality may be innate or it may have been acquired by experience of the results of previous reactions of the sort in question.

Head and Holmes[5] have brought forward some very interesting evidence that not only the affective quale of sensations, but also the emotional life in general, is functionally related to the primitive intrinsic nuclei of the thalamus, rather than to cortical activity. And certainly there is much evidence in the behavior of lower animals, especially birds, that a high degree of emotional activity is possible where the basal centers are

[5] Brain, vol. 34, p. 255, 1911.

highly elaborated but the cerebral cortex is small and very simply organized.

From all of these considerations it seems probable that the functions of the higher association centers of the cerebral cortex do not consist of the elaboration of crude sensory data or of any similar elements, but rather of the coördination and integration of highly elaborated subcortical organic circuits which in the aggregate make up the greater part of the reflex and instinctive life of the species.

NOTES

MEASURED ELECTRICAL STIMULI IN THE STUDY OF BEHAVIOR

ROBERT M. YERKES

The Martin method of measuring induction shocks has now been perfected to a point which renders it available for students of animal behavior and it seems wholly desirable that all who are engaged in this field of research should familiarize themselves with Dr. Martin's recently published book on this subject.[1]

As the author remarks in his introduction, "There are few physiological researches which do not involve artificial stimulation of tissues; and for the production of stimuli induction shocks are in most cases the first choice. They are easier to use and they subject the stimulated tissue to less permanent modification than do other forms of artificial stimulus. Induction shocks are, however, very variable in intensity; and as commonly used there is no means of knowing or of stating their physiological effectiveness in other than the most general terms. An induction shock is weak, medium, or strong. More closely than that the user does not attempt to describe it.

"This lack of knowledge as to the strengths of the stimuli employed is often a serious handicap in the prosecution of individual researches, particularly such as call for the use of stimuli of varying strengths. It also operates to make uncertain the attempts of investigators to duplicate the experiments of others.

"No one will question the desirability of being able to measure faradic stimuli, both for the sake of controlling the stimuli used in one's own experiments, and also in order that these stimuli may be so described as to enable other workers to duplicate them as occasion arises.

"The purpose of this work is to outline a system for calibrating the apparatus used in generating induction shocks, so that

[1] Martin, Ernest G. The Measurement of Induction Shocks; A Manual for the Quantitative Use of Faradic Stimuli. New York: John Wiley & Sons, 1912, pp. vii + 117.

the value of the shocks may be expressed in terms of stimulation units; these units to be applicable to any properly constructed induction apparatus, and to be based upon determinations which can be made in any ordinarily equipped physiological laboratory. The system proposed is not a new departure, but is an extension and amplification of previous systems." (l.c., p. 1 and 2.)

These statements apply to many investigations in behavior and psychology as well as to more strictly physiological investigations. Dr. Martin's method is sufficiently simple to render it easy to use and it should be carefully considered by all investigators who desire to do accurate work.

THE NATURAL HISTORY OF BIRDS

ROBERT M. YERKES

Of the thirteen volumes in the new (fourth) edition[1] of Brehm's justly famous history of animals, three of the four volumes devoted to birds have been issued. They are numbered as volumes 6, 7 and 8 in the set. All bear the date 1911, and each volume is available in half leather at the very reasonable price of 12M ($3.00).[2]

The greater part of the materials constituting the fifteen hundred pages of these volumes were gathered and prepared for publication by the late Professor William Marshall whose death in 1907 left his great task to be completed under the direction of Doctor F. Hempelmann. In his preface to the volumes, Doctor Hempelmann especially calls attention to the emphasis which has been laid, in this revised edition, upon the structural characteristics of birds and upon their systematic relations. Chief responsibility for the facts of bird behavior and psychology is placed upon the general editor, Professor Otto zur Strassen.

The first fifty pages of volume one offers an admirably clear, concise, and complete description of the structure of the bird, of its development, its general habits, instincts, intelligence and systematic relations. Thereupon follow descriptions of the various orders, suborders and families of birds.

Throughout the volumes, the text is admirably illustrated by hundreds of wood cuts, half tones, and colored plates. Neither labor nor expense has been spared in the preparation of text and illustrations.

The accounts given of representatives of the various divisions of the class aves are interesting throughout and they appear to be reliable. Naturally, the work does not give detailed infor-

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[1] A descriptive notice of this edition appeared in this Journal, vol. 1, pp. 307–8.

[2] Tierleben, Sechster Band. Die Vögel, Erster Band: Flachbrustvögel, Tauchvögel, Pinguinvögel, Sturmvögel, Storchvögel, Gänsevögel, Raubvögel. Leipzig und Wien, Bibliographisches Institut, 1911, S. xvi + 498.

Tierleben, Siebenter Band. Die Vögel, Zweiter Band: Steiszhühner, Hühnervögel, Kranichvögel, Regenpfeifervögel, Kuckucksvögel (Kuckucke). Leipzig und Wien, Bibliographisches Institut, 1911, S. xiv + 492.

Tierleben, Achter Band. Die Vögel, Dritter Band: Kuckucksvögel (Papageien), Rakenvögel. Leipzig und Wien, Bibliographisches Institut, 1911, S. xii + 472.

mation concerning all of the birds which are mentioned, but it gives valuable general information concerning a very large number of types of bird, and one may turn to these volumes for general information concerning the natural history of this group of organisms with the certainty of acquiring a large amount of useful information and of being stimulated to further study of the form and behavior of organisms.

From the point of view of the reviewer, the editors of these volumes richly deserve commendation for their intelligent and thoroughly conscientious rewriting of this portion of the great natural history. It is a work which should be rendered available in several languages. In English, we have nothing at all comparable to it and, as was suggested in our preliminary notice of the new edition, it is very much to be desired that the complete work be rendered into English.